THE CRETACEOUS REPTILE
CHAMPSOSAURUS NATATOR PARKS

BY

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INTRODUCTION

Purpose of study. The dissociated vertebral centra of *Champsosaurus*, spool-like objects with characteristic markings, are among the commonest fossils to be found in vertebrate-bearing continental deposits of late Cretaceous and early Tertiary age. The oldest known examples are from the Milk River formation of Alberta (Santonian), and the youngest are from the base of the Willwood formation (lowest Eocene) of Wyoming (Jepsen, 1930, p. 494).

The fossil collection of the National Museum of Canada contains an abundance of fragmentary remains of *Champsosaurus* from the Oldman formation ("Belly River") of the Red Deer River valley, Alberta. One excellent specimen, however, has been in the collection for some years. In 1917, Mr. G. E. Lindblad, a member of the Museum expedition under Mr. C. M. Sternberg, discovered the anterior part of a skeleton, including a well preserved skull and mandible. Preparation of this skeleton was completed by Lindblad after he rejoined the Museum staff, and it is now ready for exhibition. Before this task was completed, however, a small but well-preserved skull of *Champsosaurus* was discovered in the same general area by Mr. H. L. Shearman, a member of Lindblad's expedition of 1953. This specimen has been skilfully prepared by Shearman. During the expedition of 1954 to the Red Deer badlands, another skull was collected; this one was incomplete but revealed some details of the internal structure. Other specimens in the Museum's collection have supplied additional information.

For reasons to be discussed below, all of these specimens are referred to the species *Champsosaurus natator* Parks (1933). This species was based on an incomplete skeleton with fragmentary skull. Not only do the National Museum specimens supplement the type material of Parks, but they supply many details of structure, especially in the skull, which were not previously recorded. It is considered that this new information will be better understood if it forms part of a general osteological description, rather than a supplement to earlier accounts. Dr. Wann Langston, Jr., of the National Museum staff, has provided valuable help and advice. The excellent work of G. E. Lindblad and H. L. Shearman as collectors and preparators should also be mentioned. The photographs and drawings that accompany this report are the work of the author.

Systematic position of Champsosaurus. Cope (1876, p. 350) placed the genus in the Rhynchocephalia under a new suborder Choristodera, and this arrangement has been followed almost universally since that time. There is no doubt that *Champsosaurus* was derived from an early diapsid stock. However, there are many features that distinguish the genus from the known Rhynchocephalia. We have to decide whether these differences were derived from the early ancestors, or whether they are adaptations to a semi-aquatic, fish-eating mode of life. Romer (1945, p. 201) removed the Choristodera from the Rhynchocephalia to the Eosuchia. This is a more acceptable position, even if only because the order Eosuchia is a convenient one in which to group all primitive diapsids of uncertain derivation.

Features that Romer mentioned as distinguishing *Champsosaurus* from the Rhynchocephalia are the absence of a beak on the jaws and the presence of socketed rather than acrodont teeth. Actually the teeth are not socketed, but neither are they truly acrodont as in *Sphenodon*. Other distinguishing features that might be mentioned are as follows: presence of a secondary palate composed of premaxillae, maxillae, vomers, and a bone here called internarial; absence of a pineal opening; vertebral centra almost amphiplatyan, with no trace of the notochordal foramen; neural arch not fused to centrum. The European genus *Simoedosaurus* of Gervais is generally recognized as being closely related to *Champsosaurus* and may, in fact, be congeneric, but this question will not be dealt with here.

Species of Champsosaurus. Cope (1876) established the genus on material that he had collected from the Judith River beds of Montana. He recognized four species: *C. annectens, C. brevicollis, C. profundus,* and *C. vaccinsulensis.* The first, considered as the type of the genus, was based on a number of vertebrae not certainly belonging to one individual. The other three species were also based on vertebrae, of which only the types of *C. profundus* were believed to be from one individual. Later Cope (1881) recorded *Champsosaurus* remains from the Puerco (Lower Paleocene) of New Mexico, establishing the new species *C. australis* on a series of vertebrae. Two additional species, *C. puercensis* and *C. saponensis,* were added to the Puerco fauna by Cope in 1882.

In spite of the fact that Cope had described seven species by 1882, the nature of *Champsosaurus* could be but imperfectly known until Barnum Brown discovered three more or less complete skeletons in the "Laramie" of Montana. These were described by Brown (1905) as the types of the new species *C. laramiensis* and *C. ambulator.* In the same monograph Brown reviewed the species described by Cope, concluding that only *C. profundus, C. australis,* and *C. saponensis* were recognizable, although *C. annectens* might be redefined if new material could be discovered.

Large numbers of dissociated vertebrae of *Champsosaurus* are to be found in the badlands of the Red Deer River of Alberta, but it was not until 1927 that material adequate for a specific definition was described from this provenience. In that year W. A. Parks established *C. albertensis* for a skeleton without a skull, collected from the Edmonton formation. From the older "Belly River" (Oldman) formation, Parks (1933) described *C. natator* from an incomplete skull and parts of the skeleton, *C. inflatus* from a very incomplete skeleton without skull, and *C. inelegans* from three dissociated cervical vertebrae.

In attempting to assign the material before me to one or more of the described species of *Champsosaurus,* I have tabulated in comparative form the supposed diagnostic characters of the various species. From the results, I have concluded that distinctions based on form and proportions of the vertebrae have little practical value, whatever their theoretical significance may be. The ratios of length, height, and width change throughout the vertebral column of one individual. Without a large series of specimens we cannot evaluate even such striking features as the tapering vertebral centra of *C. inelegans.* For present purposes, therefore, I am ignoring not only those species regarded by Brown (1905) as invalid, but also *C. annectens, C. australis, C. saponensis, C. inflatus,* and *C. inelegans.*

Of the remaining species, only *C. natator* Parks is from the Oldman formation. This, therefore, is the most probable species to which the National Museum specimens might be referred. Study of these specimens fails to disclose any feature that could be used to separate them clearly from *C. natator*. Features common to the type of that species and to the present examples are: (1) relatively slender snout with expanded end; (2) posterior ends of prefrontals wedged between anterior ends of frontals. It is not clear how *C. natator* differs from *C. albertensis* Parks, of which the skull is unknown, but as the latter species is from the Edmonton formation, it is probable that differences do exist. A number of features readily distinguish the present specimens from *C. laramiensis* and *C. ambulator* of Brown. These differences are noted in appropriate places in the descriptive section.

Note on the occurrence of C. laramiensis. I have been informed by Mr. R. V. Witter, formerly of Princeton University, that he visited the site on Hell Creek, in Garfield County, Montana, from which Brown obtained the type specimens of *C. laramiensis* and *C. ambulator*, and he observed that the occurrence was stratigraphically above the Hell Creek beds and within the lower part of the Fort Union group. As these species are commonly thought of as Cretaceous in age, I reviewed the literature on the subject. Brown (1905) stated that his specimens "were found in the lower strata of the lignite, above the Ceratops Beds." Later Brown (1907) applied the name "Hell Creek Beds" to what he had previously called "Ceratops Beds." He reaffirmed the occurrence of his *Champsosaurus* skeletons in the overlying lignite beds, which had yielded no dinosaur bones, and correlated these upper strata as "Fort Union?". Brown's suggestion was ignored by Thom and Dobbin (1924) in their revision of the late Cretaceous and early Tertiary of Montana and North Dakota, for they redefined the term "Hell Creek" to include Brown's lignite beds, and placed the expanded "member", together with the overlying Tullock beds, in the Lance formation. Subsequent workers, notably Dorf (1940, p. 223), have recognized the Paleocene age of the Tullock beds and the equivalent Ludlow beds farther east. Surely Brown was also right in excluding from the Lance equivalent the "lignite beds," barren of dinosaur remains. Not only in Montana and North Dakota, but also in Saskatchewan, are dinosaur remains restricted to the beds below the lowest lignite seam. Brown should be followed in recognizing the "lignite beds" as a stratigraphic unit distinct from the underlying Hell Creek, and forming the local base of the Tertiary section. The geological age of *Champsosaurus laramiensis* and *C. ambulator* will have to be accepted, not as Cretaceous, but as Paleocene.

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SYSTEMATIC DESCRIPTION

Class Reptilia

Order **Eosuchia**

Suborder **Choristodera**

Champsosaurus natator Parks

Royal Society of Canada, Trans., ser. 3, vol. 27, sec. 4, pp. 122-131, pls. 1-5, 1933.

Type. Royal Ontario Museum No. 856, Vertebrate Palæontology Collection; incomplete skull, most of vertebral column and dorsal ribs, pelvis, and incomplete femora; from Oldman formation (Belly River series) in legal subdiv. 3, sec. 11, tp. 21, rge. 12, W. 4th mer., Red Deer River valley, Alberta; collected by L. Sternberg, 1930.

Referred specimens. These constitute the subjects of the present paper. National Museum of Canada No. 8919: anterior part of skeleton, including skull, lower jaw, vertebral column to 20th vertebra, pectoral girdle and front limbs, parasternal ribs; Oldman formation in sec. 35, tp. 20, rge. 12, W. 4th mer., south side of Little Sandhill Creek, Red Deer River valley, Alberta; collected by G. E. Lindblad under direction of C. M. Sternberg, 1917; prepared by Lindblad, 1953. N.M.C. No. 8920: small skull, almost complete, from Oldman formation, sec. 28, tp. 21, rge. 12, W. 4th mer., west side of Red Deer River, Alberta; collected by H. L. Shearman under direction of Lindblad, 1953, and prepared by Shearman. N.M.C. No. 8921: fragmentary skull, from Oldman formation, near centre of sec. 29, tp. 21, rge. 12, W. 4th mer., west side of Red Deer River valley, Alberta; collected and prepared by Lindblad, 1954. N.M.C. No. 8922: fragmentary skull and parts of skeleton, from Oldman formation, 4 miles southwest of mouth of Little Sandhill Creek, presumably in sec. 26, tp. 20, rge. 12, W. 4th mer., Red Deer River valley, Alberta; collected by C. M. Sternberg, 1917. N.M.C. No. 2785: right mandibular ramus, from Oldman formation, same locality as No. 8922; collected by C. M. Sternberg, 1917.

Specific characters. Snout relatively slender, with expanded tip; anterior ends of frontals diverging to receive posterior ends of prefrontals; postorbitals not reaching inferior temporal opening; palatal teeth in six distinct rows; vertebral centra about as wide as high; interclavicle relatively short and broad.

OSTEOLOGICAL DESCRIPTION

Skull in general. The largest skull (No. 8919, Plates II, III) is rather well preserved but is shattered in places, especially in the temporal region. There is also some distortion, the right temporal region being pushed slightly in and back, and the left temporal region down and out. The anterior end of the snout has been bent to the left. The sutures are obscure in places, especially on the ventral surface; this is partly due to imperfect preservation, partly to the mature age of the individual. Length of this skull is 475 mm., and maximum width is 215 mm.

The smallest skull (No. 8920, Plates IV, V) is essentially complete and shows no distortion, except possibly some vertical compression. The sutures

are firm and most of them are clearly visible, suggesting that the individual was mature, although not full grown. Seen in dorsal view this skull differs somewhat in outline from No. 8919; instead of the graceful pear-shape of the latter skull and of the skulls illustrated by Brown (1905), No. 8920 has the sides sweeping back in a concave curve from the postorbital region to the quadrate. Here there is a sharp change in direction, and the remaining portion of the sides, formed mostly by the squamosals, is almost straight, being directed backward and slightly inward to the posterolateral extremities. This distinctive outline is believed to be an age feature. More puzzling is the high degree of "ornamentation" on the dorsal surface of this smallest skull. In contrast, the largest skull, No. 8919, is nearly smooth, and the specimens of intermediate size are moderately ornamented. It is possible that this was the developmental pattern, the excrescences of the young skull being gradually smoothed out with increase in size. It is also possible, however, that these are individual variations. Length of skull No. 8920 is 280 mm., and its maximum width is 111 mm.

Specimen No. 8921 consists of the snout with the anterior part of the orbital rims and portions of the frontals, parietals, and exoccipitals. The palatal region is imperfect but shows details not visible on the better preserved skulls. Size, and degree of "ornamentation", are intermediate between those of No. 8919 and No. 8920.

Specimen No. 8922 consists of a fragmentary skull, including parts of the temporal and basicranial regions, together with numerous fragments. In size this skull is almost as large as No. 8919, and the dorsal surface is almost smooth, there being a suggestion of nodes along the upper edges of the parietals.

Premaxillae (*Pm*, Figures 1, 2). These bones form the anterior end of the snout. Being wider in maximum than the maxillae, they give the snout a bulbous expansion anteriorly. The sutures on the dorsal side, with the nasals and maxillae, are not clearly defined. The premaxillae form the floor and all but a small dorsal median part of the rim of the external nares, which open upward as well as forward. On the ventral side, the suture with the maxillae is transverse on No. 8919, originating from the sides of the internarial (see below) about 10 mm. from the anterior tip of that bone, whereas in No. 8920 the suture begins at midline at the anterior tip of the internarial and runs obliquely backward as well as outward. The axial portions of the premaxillae bulge downward into the oral cavity and form the anterior continuation of the median ridge on internarial and maxillae. At the anterior end of this ridge, just behind the tooth row, there is a median pit, which in No. 8920 continues as a slit-like opening into the floor of the nares. Behind this pit are two foramina, one on each premaxilla, presumably for nerves or blood vessels. The tooth row on the premaxillae is somewhat excavated, and bears large teeth, the number of which varies. In No. 8919 there are two teeth on the right and one on the left, with pits to receive five teeth from the mandible. In No. 8921 there are three teeth and three pits on each side. In No. 8920 there were at least five teeth on each premaxilla, of which the three most anterior are preserved. The interdental pits are not so large relatively, as those on the other two skulls.

Maxillae (*Mx*, Figures 1, 2, 3). These are long, narrow bones, forming the lateral portions of the snout. From the junction with the premaxillae
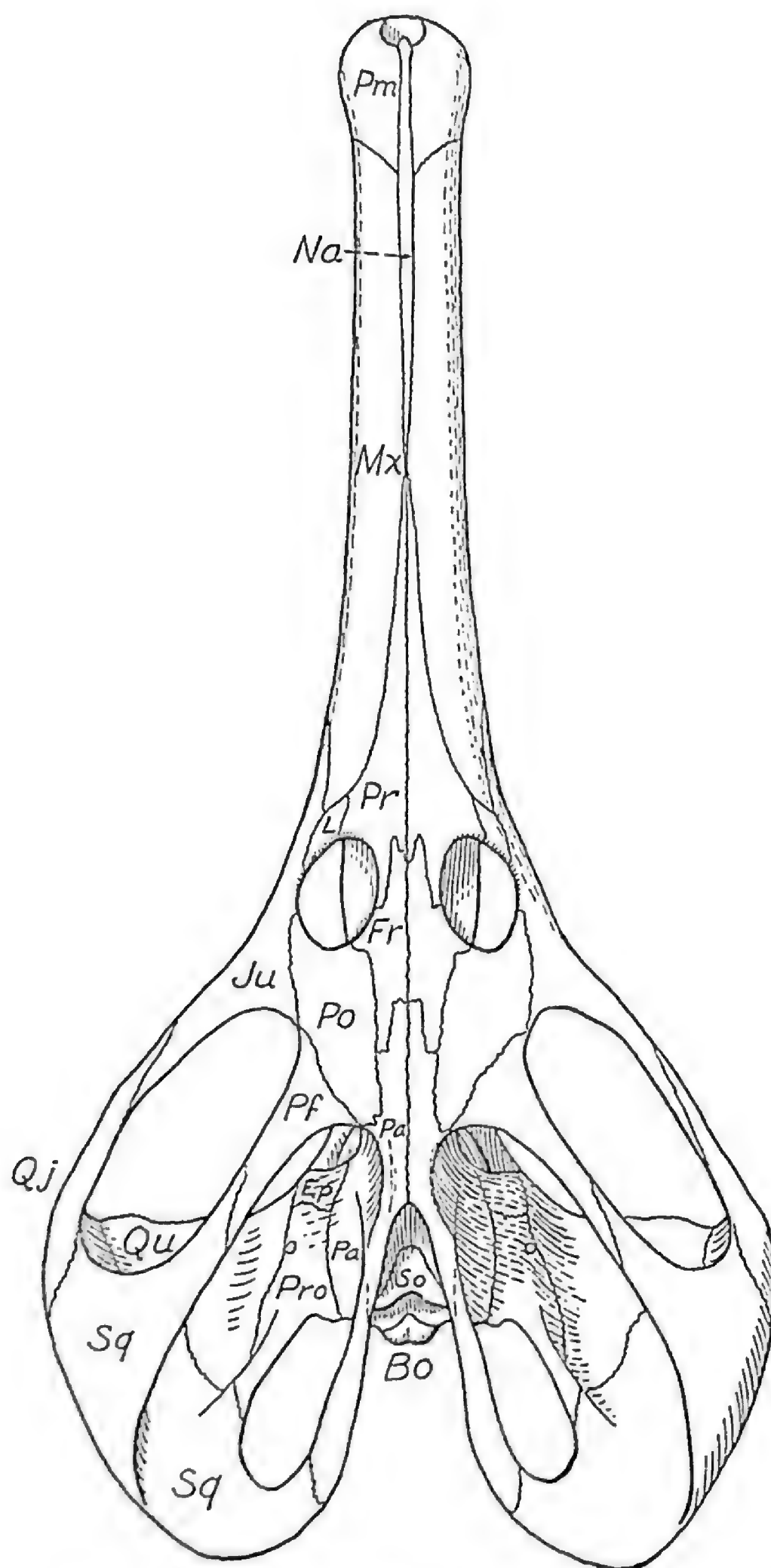
Figure 1. *Champsosaurus natator*, outline drawing of skull, dorsal view, somewhat restored. Based mainly on No. 8919, but information on sutures from No. 8920. X ⅓.

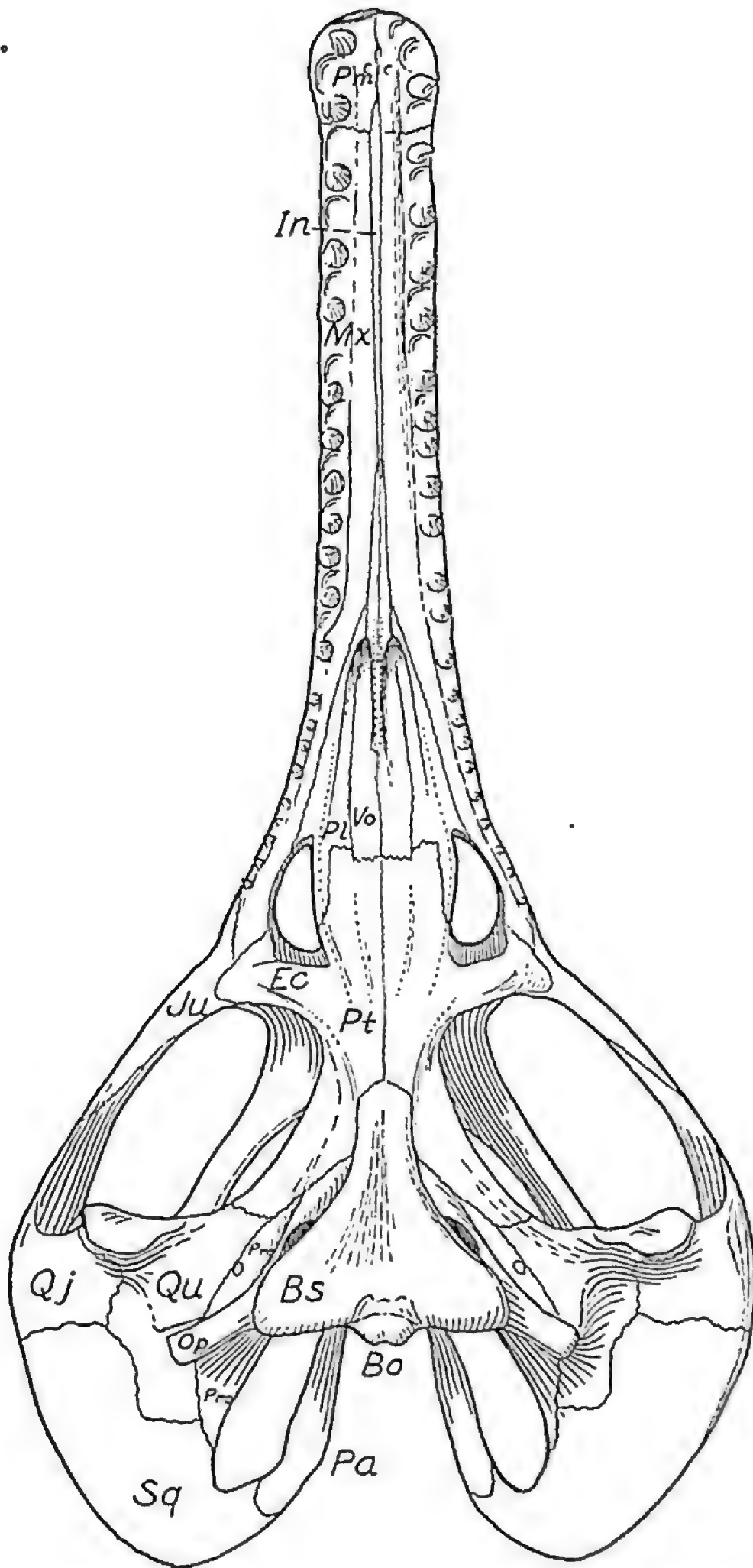Figure 2. *Champsosaurus natator*, outline drawing of skull, ventral view, somewhat restored. X ⅓.

they retain a rather uniform width for most of their length, but posteriorly they expand somewhat. In the dorsomedian area the two maxillae are separated by the narrow nasals. Farther back the prefrontals appear and gradually wedge the maxillae farther apart. They are excluded from the orbital rim by the lachrymals and jugals, between which they extend as a blunt wedge. Below the jugals the maxillae continue back as narrow dentigerous strips to meet the ectopterygoids. From this posterior termination the inner suture of the maxillae runs obliquely forward, along the margin of the palatine opening, in contact with the palatine and vomer bones, and gradually approaches midline. At the anterior termination of the vomers, the median margins of the maxillae run forward parallel to each other, narrowly separated by the internarial. This bone, with the inner edges of the maxillae, forms a median prominence along the roof of the mouth, within which are the floors of the nasal passages. There is thus a kind of secondary palate, achieved by somewhat different means than the arrangement more fully developed in the crocodiles. A cross-section of the snout (Figure 3), reconstructed from No. 8921, shows that the maxillae form the roof, floor, and outer wall of the nasal passages, and the nasals and internarial provide the inner wall. The lateral margins of the maxillae are tooth-bearing for their entire length. In No. 8919 there were about 23 teeth on the right side and 25 on the left. In No. 8920 there are at present 29 teeth on the right side and 27 on the left, and the original number was only a little larger. The teeth are of uniform size anterior to the internal nares, but behind these they become progressively smaller. No. 8919 has well-developed pits between adjacent teeth, but No. 8920 has the teeth mostly set close together.
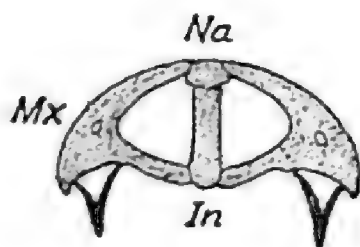

Figure 3. *Champsosaurus natator*, transverse section through snout in anterior third, based mostly on No. 8921. X 1.

Internarial (new name) (*In*, Figures 2, 3). The bone for which this name is here proposed was called ethmoid by Brown (1905, p. 11). It appears on the roof of the oral cavity as a narrow median strip lying between the two maxillae and extending from the premaxillae to the vomers. In No. 8920 it separates the anterior tips of the vomers slightly. There is no trace of a paired origin. In specimen No. 8921, where the "secondary palate" has been broken away posteriorly, the internarial is seen to have the structure shown in Figure 3. It is, in fact, a bony nasal septum, of about equal thickness throughout, extending from the roof of the mouth to the under side of the nasals. In addition to separating the two nasal passages, which could have been done by softer tissue, the internarial forms a buttress for the palatal part of the maxillae. Although Brown called this bone the ethmoid, he was not certain of its real homology. By "ethmoid" in reptiles is usually meant the sphenethmoids, which are paired bones in the anterior interorbital region. The mesethmoid of birds and mammals is more nearly analogous to the present bone, but it too lies farther back. The participation of such a bone in the roof of the mouth is apparently a unique arrange-

ment. However, it occupies the position of the cartilaginous nasal septum and paraseptal cartilages in the amniote embryo and is presumably a direct ossification of these structures. As such it would not be homologous with any other bone or bones in the vertebrate skull and therefore would require a new and distinctive name. "Internarial bone" seems to be a suitable designation, as it is both a description of the location and a paraphase of septum nasi, the name of the cartilaginous predecessor.

Nasals (*Na*, Figures 1, 3). In all three specimens these bones are completely fused into a single element. This appears on the dorsal surface of the snout as a long, narrow strip, lying between the two maxillae and extending from the external nares to the prefrontals, approximately two-thirds the length of the snout. The anterior end, when complete (as in No. 8921), projects beyond the premaxillary rim of the external nares as a slender tip. The posterior termination (No. 8920) forms a slender wedge between the anterior ends of the prefrontals. Seen in cross-section (Figure 3), the fused nasals form a wedge between the two dorsal portions of the maxillae, supported from below by the wall-like internarial. The lower surface, which meets the upper edge of the internarial, bears a narrow median ridge which apparently keys into a corresponding groove on the internarial.

Prefrontals (*Pr*, Figure 1). These are tapering bones. As seen on the dorsal surface of the skull, they begin as slender points at the posterior tip of the nasals. Widening rather regularly (No. 8921), they extend back to the anteromedian margin of the orbits. The suture with the frontal shows some variation. In No. 8919 it begins at the midline suture at a point about opposite the midlength point of the orbits. From here it runs forward and slightly outward to a point nearly opposite the anterior end of the orbit, then turns sharply backward and curves outward to the orbital rim well behind orbital midlength. Thus each prefrontal embraces a narrow prolongation of the corresponding frontal, and the two frontals receive between them the posterior ends of the prefrontals. In specimen No. 8921 the arrangement is similar except that the suture is more sinuous. No. 8920 has a very sinuous suture, especially the part adjacent to midline. The portion of the orbital rim formed by the prefrontals is essentially smooth in No. 8919, moderately nodose in No. 8921, and strongly nodose in No. 8920. In No. 8921 the prefrontal-lachrymal suture reaches the orbital rim over the top of a large prominence, whereas in No. 8921 it goes through a groove between two nodes. The nodular area along the median margin of the orbits is formed in part by the prefrontals, in part by the frontals, the suture winding over the apices of the nodes. Within the orbits the prefrontals form the anterointernal quarter of the wall. The suture with the lachrymals winds down the anterior wall of the orbit, then turns outward to the maxillae. The suture with the frontals goes directly down the median orbital wall, then curves abruptly forward to the anterior ventral tip of the frontals, then back to the midline. Like the frontals, the prefrontals are heavy and deep in the interorbital region. Farther forward they form the dorsal and most of the lateral wall of the large, semicircular olfactory foramen.

Lachrymals (*L*, Figure 1). These are small triangular bones, wedged between the prefrontals on the median side, and the maxillae and jugals on the lateral side. They form part of the anterior border of the orbits. On

specimen No. 8919 the sutures are obscure, but on Nos. 8920 and 8921 they are clearly visible. As seen on the dorsal surface of the skull, each lachrymal begins at a point along the prefrontal-maxillary suture. From here the suture with the prefrontal runs directly back to the orbit, passing through the rugose rim. The suture with the maxilla runs obliquely backward and downward to meet the upper side of the anterior branch of the jugal, along which it then continues to the orbit. In specimen No. 8921, breakage reveals that the lachrymals extend forward as a tapering extension beneath the prefrontal-maxillary suture, the surface of contact with the overlying bones being deeply striated. Within the orbit the lachrymal appears as a broad wedge between the prefrontal and palatine, the lowest point being on a level with, and slightly median to the lachrymal foramen. This opening lies within the orbit, between lachrymal and palatine, with the jugal wedging into the outer margin. The external opening of this duct is obscure, but apparently located at the junction of lachrymal, maxilla, and jugal. The passage may also open into the olfactory cavity, between maxilla and palatine.

Jugals (*Ju*, Figures 1, 2). These are slender bones, forming the dorsal part of the suborbital bar. The anterior end is tapered, wedged between two parts of the maxillae, and is in contact dorsally with the lachrymals. Behind the orbits the jugals meet the postorbitals; the suture is directed obliquely inward as well as backward, bringing the jugals into the anterior border of the inferior temporal openings. Beneath the cranial roof this part of the jugals is in contact with the postfrontals.

Postorbitals (*Po*, Figure 1). Triangular bones forming the posterior part of the orbital rim, the postorbitals are smooth in No. 8919 and moderately rugose and striate in No. 8920. In the latter specimen the dorsal sutures of each postorbital can be clearly seen to converge toward the anteromedian corner of the superior temporal opening, forming a boundary with the frontal medially and with the jugal and postfrontal laterally. The postorbitals are excluded by the jugals from the margin of the inferior temporal openings but in turn separate the frontals from the postfrontals (compare with Brown's description of the postorbitals in *C. laramiensis*). The ventral disposition of the postorbitals is similar to the dorsal; from a wide portion in the posterior wall of the orbits the bones taper back to the superior temporal openings, forming a small portion of the rim at the anteromedian corner.

Frontals (*Fr*, Figure 1). These narrow bones form the cranial roof from the orbital region to the junction with the parietals. Between the orbits they form, with the prefrontals, a low arch, which is smooth in No. 8919, rugose in No. 8920 and No. 8921. Posteriorly the frontals are saddle-shaped, gently concave anteroposteriorly, and arched from side to side. On No. 8920 this area is longitudinally striate. The peculiar re-entrant suture with the prefrontals has been described. Posteriorly the frontals are deeply notched to receive an anteromedian prolongation of the parietals. Laterally the frontals are in contact only with the postorbitals. On the ventral side there is an anterior prolongation of each frontal, lapping against the prefrontal and forming part of the wall of the olfactory opening. The top of this opening continues back along the ventral surface of the frontals as a gradually constricting groove which opens out again in the postorbital region. Here, a low rounded ridge appears from the median ventral surface

of the frontals and continues back onto the parietals. The ventral relationships of frontals and parietals are similar to those on the dorsal surface.

Postfrontals (*Pf*, Figure 1). These form the anterior part of the upper temporal arches. They are cut off from the frontals by the posterior extension of the postorbitals. On the arch they are flat strips of bone, smooth in No. 8919, but with incipient nodes on No. 8920. The posterior suture with the squamosals is obscure in No. 8919. In No. 8920 it can be seen clearly as a very oblique line of contact extending backward and upward from the margin of the inferior temporal opening to the superior temporal opening.
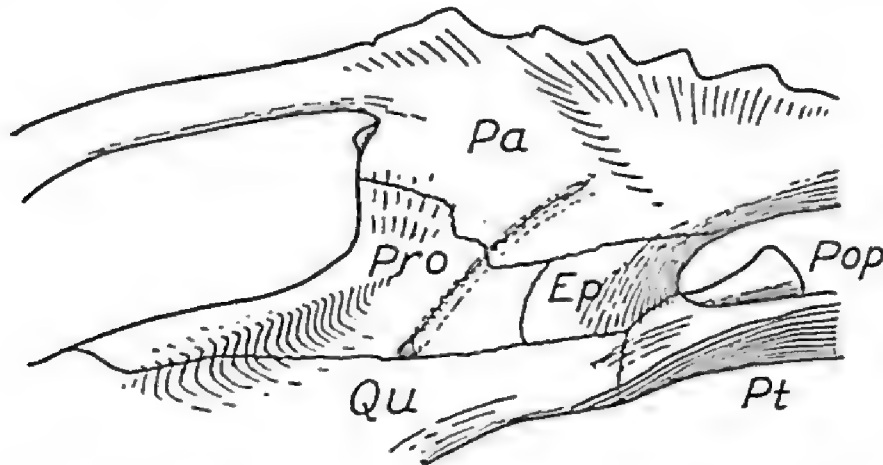

Figure 4. *Champsosaurus natator*, right temporal region, lateral view, with temporal arches removed, based mainly on No. 8920. X 1.

Parietals (*Pa*, Figures 1, 2, 4). In addition to their normal position in the posterior cranial roof, the parietals have a slender, flat, posterior process which forms most of the median margin of the superior temporal opening. This process laps obliquely against a process of the squamosals and completes this temporal arch. Coming back to the main part of the parietals, the dorsal surface of this is noticeably elevated along its margins and depressed along the midline. The lateral ridges are smooth in No. 8919, rugose in No. 8921, and have a series of prominences which form a serrate outline in No. 8920. There is no trace of a pineal opening. Anteriorly the parietals form a blunt wedge between the posterior ends of the frontals. The suture continues backward, then outward, to the rim of the superior temporal opening. The lateral surface of the parietals slopes downward and outward from the lateral ridge, to overlap the opisthotics along a nearly horizontal line. The anterior edge of this lateral wall of the parietals forms a large part of the margin of the vacuity through which the brain emerged from the bony cranium. Presumably the lateral walls of the brain cavity were cartilaginous farther forward. On the external surface of the lateral part of the parietals, that is, on the inner wall of the superior temporal openings, there is a low but distinct ridge extending downward and slightly forward from the high point of the parietal crest. This is presumed to mark the boundary between a small anterior and a large posterior portion of the temporal muscles. In ventral aspect (No. 8921) the parietals may be seen to meet the frontals along a suture corresponding to that on the dorsal surface. The low median ridge, mentioned in the description of the frontals, extends onto the parietals for about half the length of these bones. Where this ridge disappears, the cranial roof bulges upward to form a rounded impression, apparently to receive the dorsal part of the cerebellum. Behind this, again the cranial roof is a simple arch, not perforated by any foramina.

Proötics (*Pro*, Figures 1, 2, 4). Although not differentiated from the squamosals by Brown, these bones are clearly distinct in No. 8920. They form a posterior portion of the inner wall of the superior temporal vacuity. On the median side they are in sutural contact with the descending portion of the parietals. Anteriorly they are joined by a sinuous suture to the epipterygoids. They have a long lateral suture with the quadrates, behind which they come in contact with the squamosals. These posterior extensions of the proötics form the dorsal rim of the occipital surface, below which they form a triangular area, bounded behind by the squamosal and in front by the paroccipital process of the opisthotics. On the ventral surface of the skull the proötics extend forward as a narrow strip separating the quadrates from the opisthotics, but are narrowly excluded from the external auditory meatus by a thin wall of the opisthotics. Posterior to this the proötics are pierced by an oval foramen, which emerges on the dorsal surface close to the suture with the quadrate. Within this foramen there is a much smaller opening posteriorly into the proötic. It is probable that these foramina were for the passage of the external carotid artery and the seventh cranial nerve.

Epipterygoids (*Ep*, Figures 1, 4). Dorsally these continue the wall of the superior temporal vacuity forward from the proötics but contribute a much smaller area. Their suture with the parietals is a forward continuation of the proötic-parietal suture. Below, the epipterygoids meet a narrow anterior prolongation of the quadrates and a posterior branch of the pterygoids. The anterior margin is free and forms part of the rim of the large trigeminal foramen. The identification of these bones as the epipterygoids may be questioned, as it might seem more proper to apply this name to the slender bones described below as postoptics. If this is done, however, the subjects of the present paragraph are left without a name, as they are clearly distinct from the proötics that lie farther back.

Squamosals (*Sq*, Figures 1, 2). These are bones of complex shape, which form the posterolateral corners of the skull and contribute to the temporal arches. In dorsal view they are seen to form the posterior part of the floor of the temporal fossa, and meet the proötics, quadrates, and quadratojugals along a sinuous suture. From the posterior extremity a process curves inward and forward to meet the posterior extension of the parietals, and forms the posterior temporal arch. The lateral portion of the squamosals curves upward, then obliquely inward and forward, and narrows to form the posterior half of the superior temporal arch. The anterior edge of this lateral portion meets the quadratojugals along an anteroposteriorly directed suture at the posterior base of the inferior temporal arch. In ventral view the squamosals are seen to form the posterolateral part of a shallow fossa which housed the depressor mandibuli, the reptilian equivalent of the digastric muscle. On this surface may be seen the suture with the quadratojugal in front and the quadrate and proötic on the inner side. The posterior extremity of the quadrates is received into a shallow pocket on the edge of the squamosals.

Quadrates (*Qu*, Figures 1, 2, 4). These form a large anterior portion of the floor of the temporal fossa, between epipterygoids and proötics on the inner side and quadratojugals and squamosals on the outer. In ventral view they show the condyle for articulation with the lower jaw, a saddle-shaped prominence which is narrow anteroposteriorly and wide medio-

laterally. Behind the condyle the ventral surface forms part of the shallow fossa for the depressor mandibuli muscle.

Quadratojugals (*Qj*, Figures 1, 2). The main part of these bones is slender, forming much of the lower temporal arch. Posteriorly they are expanded, meeting the squamosals and quadrates and forming a corner of the "digastric" fossa. The suture with the jugals crosses the lower temporal arch very obliquely, from posterodorsal to anteroventral.

Supraoccipital (*So*, Figure 1). This appears as a distinct bone on specimen No. 8920. It is small and lies deep in the notch formed by the two posterior extensions of the parietals, forming a shelf over the top of the foramen magnum. Its posterior or foraminal margin is broadly notched. The anterior suture with the parietals is an overlapping one, parietals on supraoccipital. The posterolateral angles meet the upper part of the exoccipitals. This bone is commonly designated dermosupraoccipital, on the grounds that it is of dermal origin and therefore not the equivalent of the supraoccipital in the Anamnia.

Exoccipitals. These form the lateral walls of the foramen magnum. Dorsally, behind the suture with the supraoccipital, each exoccipital projects backward, and forms, as noted by Brown, a pair of articular flanges for the first vertebra. Below this projection, the posterior surface of the exoccipital is somewhat excavated. In the lower lateral part of this surface are two foramina, of which the upper is regarded as the condylar foramen, for the twelfth nerve, and the lower as the jugalar foramen, for the tenth nerve.

Opisthotics (paroccipitals) (*Op*, Figure 2). Brown (1905, p. 12) described these bones as part of the exoccipitals, which they are in many reptiles. In both specimens, No. 8919 and No. 8920, the sutural boundary with the exoccipitals is distinct. It follows a slightly irregular course down the occipital surface just lateral to the two neural foramina mentioned above. The opisthotics emerge as cylindroid processes from between the exoccipitals and the proötics, and extend obliquely outward, backward, and slightly downward along the posteroventral surface of the proötics. The posterior end is roughly truncated and forms an important point of attachment for anterior neck muscles. Medially, along the suture with the exoccipitals, there are two foramina, one of which probably received the internal carotid artery. The opisthotics on the ventral surface of the skull extend forward between proötics and pterygoids laterally and basioccipitals and basisphenoid medially. The suture with the basioccipitals is obscure. An external auditory meatus is situated at the two posterolateral angles of the basisphenoid, and is partly concealed by this bone in ventral view. These are large oval openings seemingly bounded medially by the basisphenoid and laterally by a thin wall of the opisthotics.

Basioccipital (*Bo*, Figures 1, 2). This forms the occipital condyle. The suture with the exoccipitals begins well within the foramen magnum, the two sides diverging gradually toward the rim of the foramen, then turning sharply outward and downward. From this point the suture lies in a narrow but distinct groove (No. 8920). The condyle is a rounded knob, slightly impressed with a median groove on the upper posterior surface. There is a broad groove bounding the condyle ventrally. Below this again the posteromedian margin of the basioccipitals is broadly excavated

medially. The ventral surface of the bone passes in above the basisphenoid; its forward extension is concealed in Nos. 8919 and 8920, and broken away in No. 8922.

Basisphenoid (*Bs*, Figure 2). This is a triangular bone, spreading out posteriorly to overlap the basioccipital below. It narrows rapidly in the vicinity of the external auditory meatus and extends forward as a narrow bar of bone between the posterior branches of the pterygoids. It ends anteriorly in a transverse, serrate suture with the median portion of the pterygoids. The ventral surface of the basisphenoid is concave posteriorly and shallowly grooved anteriorly. The dorsal surface of the basisphenoid that is overlain by the basioccipital is broadly keeled (No. 8922), in correspondence with the concavity on the ventral surface. Farther forward the dorsal surface of the basisphenoid is concave from side to side, forming part of the floor of the brain case. Near the front end is the pituitary fossa, a partly double pit directed backward as well as downward into the bone. Behind this is a second, much shallower depression, with two small adjacent foramina, one on each side. In front of the pituitary fossa the end of the bone is elevated, and beneath this part are a pair of pockets extending back into the bone, one on each side of midline. The anterior tip is bluntly pointed, and lies between the pterygoids.

Postoptics (*Pop*, Figure 4). This term is applied to problematical bones that lie above the anterior portion of the basisphenoid. They appear to rise near the front end of the opisthotics and project forward and slightly upward as slender wings into the open area in front of the bony cranial wall. The oval space between these bones and the anteroventral edge of the parietals is believed to represent the trigeminal foramen, even though it is not closed anteriorly. It is for this reason that the bones are identified as postoptics (laterosphenoids), which are cartilage bones that are well developed in the crocodiles and some other reptiles, where they form the anterior lateral walls of the brain case between the optic and trigeminal foramina. The bones in *Champsosaurus* have the appearance of osseous buttresses of a cartilaginous wall. They could easily be lost in fossil skulls, but are well shown in No. 8920.

Pterygoids (*Pt*, Figures 2, 4). These bones have a complex shape. The posterior branch extends diagonally backward along the side of the anterior part of the basisphenoid; more posteriorly it is separated from the basisphenoid by the anterior end of the opisthotics. The junction with the quadrates is oblique, the pterygoids overlapping backward on the ventral surface and the quadrates overlapping forward on the dorsal. The pterygoid-quadrate suture is farther forward on the ventral surface than on the dorsal. Anteriorly the pterygoids spread out as a broad platform, constituting the floor of the interorbital region and the posterior roof of the mouth. The suture with the palatines begins laterally near the posterior end of the inner margin of the palatine vacuity. From here it runs forward and inward to a point opposite the front end of the palatine vacuity, then by a zig-zag course toward the midline, becoming the vomer-pterygoid suture before intersecting the midline suture. Owing to the thinness of the pterygoids, the path of this anterior suture is essentially the same in dorsal as in ventral view. In specimens No. 8920 and No. 8922 there is a small median vacuity along the midline suture of the pterygoids, about opposite the posterior end

of the palatine vacuity. This small opening in No. 8920 is partly closed by delicate struts of bone; it probably represents incomplete ossification. The pterygoids each bear two rows of small teeth on the palatal surface, the outer row nearly marginal, the inner near the midline. Anteriorly the four rows are about equally spaced, but posteriorly the two on each side converge and ultimately unite.

Ectopterygoids (*Ec*, Figure 2). These are small, strut-like bones joining the pterygoids to the maxilla-jugal bars, and separating the palatine vacuities from the temporal fossae. Each ectopterygoid arises from the lateral margin of the pterygoid near the posterior end of the tooth rows, but the suture is obscure. From here the ectopterygoid extends outward and forward, and finally upward, to expand and meet the maxilla, the jugal, and the postorbital. There is a tooth row on each ectopterygoid, extending obliquely forward and outward across the ventral surface from near the junction with the pterygoid, and continuing posteriorly on the pterygoid as a narrow, toothless ridge.

Palatines (*Pl*, Figure 2). These are narrow bones, forming part of the oral roof in front of the pterygoids and between vomers and maxillae. The sutures with maxillae and pterygoids have been described. The line of junction with the vomers disappears into the internal nares, then reappears on the roof of the nares and continues back in the narial groove to meet the suture with the pterygoids. The narial grooves are trough-like posterior continuations of the internal nares and are formed by the palatines laterally and the vomers medially. Along the lateral margin of each groove the palatine forms a keel-like ridge which bears a single row of small teeth posteriorly but is toothless in its anterior half.

Vomers (*Vo*, Figure 2). These form the axial portion of the palate from internarial back to the pterygoids. The junction with the pterygoids is narrow. In front of this the vomers gradually twist to form the inner walls of the narial grooves, which were described above. Between the two grooves the vomers form a narrow flat strip, with a row of small teeth on either side of the midline suture. The narial grooves pass abruptly into the internal nares where this median strip expands to join with the anterior tips of the palatines in forming a floor for the nasal passages. In front of the nares the vomers, forming part of the oral roof, gradually narrow to points, which are separated from each other at their extremity by the posterior end of the internarial bone. The tooth rows on the vomers between the narial grooves continue forward on the pre-narial part of the bones. There may also be a few teeth on the posterior part of the vomers. The problem of the relationships of the reptilian vomers to the single mammalian vomer has been discussed by numerous authors. The opinions of Broom (1904) have been particularly influential. He advocated the view that the paired vomers of reptiles are represented in the mammalian skull by the posterior processes of the premaxillae. The mammalian vomer, in this interpretation, is derived from the anterior portion of the parasphenoid. It ought to be possible to settle this problem by a study of the cynodont palate, where the transitional condition might be expected, but so far the evidence from this source is not conclusive. Some students see in the cynodonts a transition from the paired "prevomers" of reptiles to the true vomer of mammals. In view of this uncertainty the older usage of vomer for the paired reptilian bones is retained here.
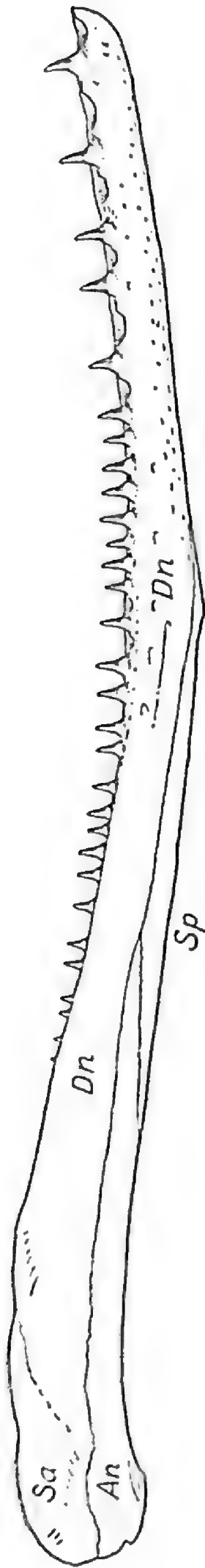
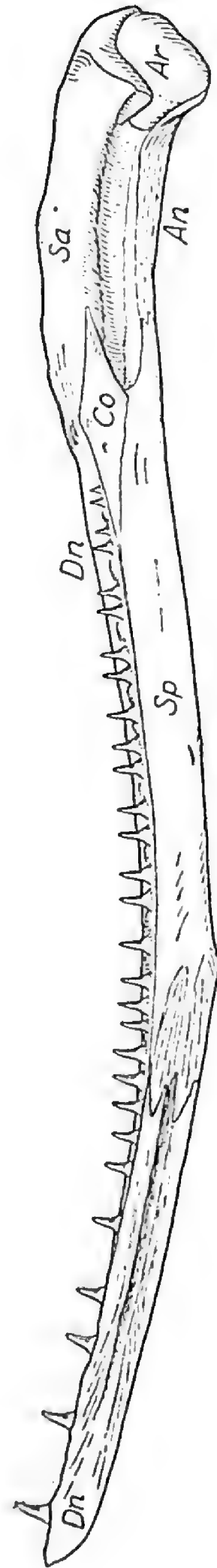Figure 5. *Champsosaurus natator*, right mandibular ramus, external view, based on No. 8919, with teeth restored. X ½.

Figure 6. Same as figure 5, internal view. X ½.

Mandible (Figures 5, 6). This is a slender and relatively delicate structure, Y-shaped in dorsal or ventral view. The symphysis extends for about the anterior two-fifths of the total jaw length. Behind this the two rami diverge gracefully toward the posterior end, where they curve downward and finally inward. This brings the articular surface into a position to compensate for the curvature of the rami and to form, with the quadrates, an efficient hinge mechanism. The disposition of the various mandibular bones is essentially as described by Brown (1905, p. 13) for *C. laramiensis*, and will be only summarized here. Length of the mandible, measured between parallels, is 380 mm., and maximum width is 180 mm.

Dentaries (Dn). Each dentary is very long, extending from the anterior tip of the ramus almost to the posterior end. It bears the tooth row, and forms most of the external surface of the ramus. The symphysis is formed by the dentaries with a small contribution by the splenials posteriorly. Along the symphysial face is a Meckelian groove, extending from beneath the splenial almost to the anterior tip of the dentary. With the two dentaries in contact, these grooves come together to form a tubular canal. The posterior dorsal end of the dentary is deeply striate, as is the adjacent part of the surangular, forming the attachment area for the temporal muscle. As on the skull, the number of teeth is variable. On specimen No. 2785 there were 31 teeth on the right ramus, most of which are now represented by the broken bases. There are 13 pits between teeth, those at the front of the jaw being large.

Splenials (Sp). The splenial forms most of the inner surface of the ramus, and extends from the posterior part of the symphysis to the Meckelian orifice. The suture with the dentary on the median side runs along the edge of the tooth row. The splenial also extends onto the lateral surface of the ramus, the suture with the dentary appearing just in front of the posterior end of the symphysis and rising gradually backward until it meets the angular, then turning down at a low angle to the inferior surface of the ramus.

Coronoids (Co). The coronoid is a slender, diamond-shaped bone on the dorsomedian surface of the ramus. Anteriorly it forms a narrow wedge between the dentary and splenial; posteriorly it lies between upper and lower parts of the surangular. The striated area on the dentary and surangular extends onto the coronoid, forming an attachment area for the inner part of the temporal muscle.

Surangulars (Sa). These form a posterodorsal part of each ramus, but the boundaries are mostly obscure. The dorsal part of the suture with the dentary is believed to be in the heavily striated area just behind the tooth row. From here the suture follows the dorsolateral edge of the ramus backward, then turns somewhat downward across the external face. It cuts off the dentary from the posterior end of the ramus, but the exact course here has not been traced. On the median side of the ramus the surangular forms the upper edge and a large part of the posterior Meckelian groove. At the rear the surangular surrounds the articular, dorsally and laterally, and forms the posterodorsal extremity of the ramus. It has a curious thin flange that extends mediad from just below the dorsal rim of the Meckelian groove and above the anterior portion of the articular.

Angulars (*An*). The angular meets the splenial on outer and inner sides of the ramus. On the outer side it is in contact dorsally with the dentary and surangular and on the inner with the surangular, forming the lower part of the Meckelian groove. Posteriorly it borders the articular on lower and inner sides, with a sharp edge that almost meets the flange from the surangular.

Articulars (*Ar*). The lumpy articular contrasts markedly with the slender or platy dermal bones of the mandible. The shape is roughly that of an oblique cone, which is wedged into the posterior part of the Meckelian groove between surangular and angular. The posterior surface, for articulation with the quadrate, faces upward, backward, and inward. An interior portion of the articular is exposed on the inner side, in the gap between surangular and angular.

Teeth in general. Some account of the distribution and number of teeth has been given above in the description of various bones. The marginal teeth, on premaxillae, maxillae, and dentaries, are much larger than the palatal teeth, and are narrowly conoid in form. The base is broad, but the sides narrow abruptly to a slender crown. In cross-section these teeth are nearly circular, but near the tip there is a slight development of cutting edges, one on the anterior, one on the posterior slope; or, on the premaxillary teeth, on median and lateral slopes. There is a slight recurve to the crown of the tooth, especially marked on the premaxillary teeth. Where the teeth have been broken away at the roots, each root is seen to be a thin circular wall, partly embraced by, partly fused with, a shallow pit in the dentigerous bone. The teeth are thus intermediate between the acrodont and thecodont condition. The pulp cavity of the tooth, which is wide in the basal part, extends into the crown but narrows rapidly, so that the walls of the crown are relatively thick. The palatal teeth, which occur in rows on the vomers, palatines, pterygoids, and ectopterygoids, are much smaller and relatively less slender. They seem more intimately fused with the dentigerous bone.

Cervical vertebrae (Plate VII; Plate VIII, figs. 1-8). The atlas is not represented. The second vertebra (axis) is represented by the hypocentrum, slightly broken on the right side, and by the complete neural arch. The hypocentrum, seen from in front, is crescentic; in dorsal view it is ovoid. The ventral surface is smoothly rounded. The dorsal surface is saddle-shaped, convex fore-and-aft, concave transversely. This surface is made up of three articular areas, for the hypocentrum and centrum of the atlas, and the centrum of the axis. The anterolateral angle projects as a blunt process, behind which is an excavation, part of the articular facette for the first cervical rib. The neural arch evidently lapped well down on the centrum as blunt diapophyses. The spine is directed almost horizontally, rising very slightly from front to back. The well-defined postzygopophyses project back some distance behind the arch and face downward and only a little outward. The neural canal is ovoid in cross-section, higher than wide. The remaining seven cervical vertebrae are complete except for the hypocentra, which are not represented. The centrum of each of these vertebrae is subcylindrical, with a distinct ventral keel. All have well developed diapophyses, those on the ninth being massive. Parapophyses appear on the fifth cervical, and become progressively more prominent, but are well

separated from the diapophyses even on the ninth vertebra. The arch becomes more solid as the diapophyses increase in size. The shape of the neural canal changes from ovoid to subcircular. The spines increase in size regularly; they project upward from the arch, but curve backward distally. The posterior overhang of the postzygopophyses becomes progressively reduced. In natural articulation the cervical series is broadly curved, with the concave side of the curve the upper one.

Dorsal vertebrae (Plate VIII, figs. 9-16; Plate IX; Plate X, figs. 1-8). Only 11 dorsal vertebrae are preserved, but all are complete except the last, which lacks the postzygopophyses. The diapophyses and parapophyses are essentially confluent on all. Each centrum is cylindrical, with concave sides. The first four dorsals have a ventral keel, but this is obscure on the fifth and absent on the remainder. Height of the spine increases slightly, then decreases; the direction changes from a posterior curve, as in the cervicals, to nearly vertical. The neural canal is slightly higher than wide.

Measurements

		mm.
Axis, hypocentrum:	length	17.1
	width, estimated	12.1
	height	11.1
	width at diapophyses	c.30
	length of neural arch	c.35
Third vertebra:	height	59.5
	height of centrum	28.7
	length of centrum	28.6
	width of centrum (posterior)	26.8
	length of neural arch	36.4
	width of neural arch	35.2
	vertical diameter of neural arch	10.2
	horizontal diameter of neural arch	7.5
Sixth vertebra:	height	72.3
	height of centrum	29.6
	length of centrum	29.0
	width of centrum (parapophyses)	29.8
	length of neural arch	47.3
	width of neural arch	38.9
	vertical diameter of neural canal	8.7
	horizontal diameter of neural canal	7.7
Ninth vertebra:	height	67
	height of centrum	28.7
	length of centrum	28.4
	width of centrum (parapophyses)	39.7
	length of neural arch	53
	width of neural arch	47.6
	vertical diameter of neural canal	7.6
	horizontal diameter of neural canal	8.3
Fifteenth vertebra:	height	74
	height of centrum	28.7
	length of centrum	30.9
	width of centrum (parapophyses)	40.3
	length of neural arch	47
	width of neural arch	47.5
	vertical diameter of neural canal	8.2
	horizontal diameter of neural canal	6.8
Twentieth vertebra:	height	69.5
	length of centrum	31.6
	width of centrum (parapophyses)	39.2
	width of neural arch	47.1
	vertical diameter of neural canal	8.6
	horizontal diameter of neural canal	8.2

Cervical ribs (Plate X, figs. 10-12). There are eight pairs of these, the ones on the left being better preserved than the others. The first rib is nearly straight and is the simplest in form. It is obliquely Y-shaped, with the bluntly pointed head continuing the axis of the shaft, and the tubercle, which is truncated, set off at an angle. The second to fifth ribs are similar, increasing in size slowly from front to rear. They are only slightly curved. The head on these ribs is slender, whereas the tubercle is robust, with an ovoid articular end. Above the anteroexternal margin there is a keel, which continues into a spine-like process projecting between head and tubercle, but closer to the head. The sixth rib resembles the fifth, is only a little larger, but has a rudimentary uncinate prominence on the posterior margin, about one-third of rib length from the distal end. This prominence is larger on the seventh rib, and makes the distal end of the shaft very broad. The eighth rib is much longer than the seventh, but the added length is distal to the uncinate prominence; the head and tubercle are close together but not confluent, the articular area of the tubercle being much the larger.

Measurements

		mm.
First rib:	length	36.0
	width (between head and tubercle)	15.7
Second rib:	length	36.6
	width	21.2
Third rib:	length	36.8
	width	21.2
Fourth rib:	length	44.6
	width	24.0
Fifth rib:	length	52.8
	width	26.5
Sixth rib:	length	57.1
	width	24.9
Seventh rib:	length	64.2
	width	25.6
Eighth rib:	length (measured as the chord of the arc)	88.2
	width	26.1

Dorsal ribs (Plate X, figs. 13-16; Plate XI, figs. 1-6). There are ten pairs of these present, that is, the ninth to eighteenth of the whole series. There is not much change in length from front to rear. The head and tubercle are confluent on all, forming an articular area with an hour-glass outline. At about midlength the shaft is ovoid in cross-section, slightly angulate along anterior and posterior sides. The distal end of the shaft is more or less expanded. The uncinate prominence is distinct on the ninth and tenth ribs, rudimentary on the eleventh, and absent from the remainder.

Measurements

		mm.
Thirteenth rib:	length (measured as the chord of the arc)	125
	width, proximal end	23.6
Eighteenth rib:	length	117
	width	22.3

Parasternal ribs. These are well described by Brown (1905, p. 21) for *C. laramiensis.* On specimen No. 8919 they were preserved in natural position for about 175 mm. along the ventral midline of the body. About

18 segments are represented. Each segment consists of a median rib and two lateral ribs. All are ovoid in cross-section. They are of uniform width everywhere except at the tips and the thickened middle. The median rib has a broad double S-curve, the middle portion being concave forward. The first median rib has an anterior projection at the middle. The lateral ribs are simply curved, convex forward, and are closely appressed for about half of their length to the anterior side of the median rib. In some lateral ribs the distal end is slightly curved downward and a little bulbous. Irregularities in the arrangement of these ribs occur in some segments, but this may be due to injury.

Measurements

	mm.
Length of a nearly complete median rib	194
Maximum diameter of same rib at midlength	7.8
Length of a nearly complete lateral rib	104

Clavicles and interclavicle (Plate XI, figs. 7, 8). These three bones are closely fused, but the sutures are visible on the dorsal side. Together they form a Y-shaped bone, with the lateral ends of the clavicles turned dorsally to parallel the anterior margin of the scapulae. These ends are slender and pointed. On the transverse portion there is a distinct thickening on either side of midline; here the clavicles meet the interclavicle along an oblique suture, now closed, which begins near the midline on the ventral side and extends some distance laterally on the dorsal side. The anterior margin is shallowly excavated near the midline. The posterior branch of the interclavicle is flat and blade-shaped, with an ovoid outline which terminates in a blunt point posteriorly.

Measurements

	mm.
Width between lateral extremities of clavicles	225
Length of interclavicle along midline	130
Maximum width of posterior branch of interclavicle	41.8

Scapulae and coracoids (Plate XII, figs. 1, 2). Each scapula and coracoid are fused together, but the suture remains distinct, extending as a nearly straight line from the glenoid cavity to the median margin. The scapula is L-shaped, with a short posterior branch and a long dorsal branch. The posterior branch is expanded, thickened on its outer side, thin on the inner side, and concave on the ventral surface. The dorsal branch is directed outward and forward as well as upward; it retains a uniform width and thickness throughout. The upper end is cut off abruptly along a broadly curved margin, suggesting a cartilaginous extension. The coracoid is ovoid in outline, with the postglenoid margin straight and the median and posterior margins broadly curved. With the scapula in natural contact with the clavicle, the median margin of the coracoid does not reach to the interclavicle. Evidently there was a cartilaginous filling, as in lizards. The coracoid is pierced by the supracoracoid foramen, near the suture with the scapula and at about mid-width of the coracoid. The glenoid cavity is

about equally shared by scapula and coracoid. It is a deeply curved notch, almost flat transversely, facing somewhat downward as well as outward.

Measurements

		mm.
Left scapula:	maximum length	100
	maximum width	47.5
Left coracoid:	maximum length	90
	maximum width	71.8

Humeri (Plate XII, figs. 3, 4). The axis of the humerus is almost straight, but the ends are well expanded. The proximal end is curved in the preaxial-postaxial plane, but flattened in the dorsoventral plane. The tuberosities are moderately prominent. The shaft at midlength is ovoid in cross-section, with the greater diameter in the dorsoventral direction. The articular edge of the distal end of the bone is nearly straight. There is a slight development of the radial condyle. The ectepicondylar foramen is represented by a narrow groove on the postaxial surface dorsal to the radial condyle; this groove deepens distally but does not penetrate to the preaxial side.

Measurements

		mm.
Left humerus:	length................................	131
	maximum width, proximal end.........	42.4
	maximum width, distal end............	53.2

Radii (Plate XII, figs. 6, 7). The radius is a slender, arcuate bone, concave along its external surface, convex on the internal surface. The proximal end is only a little expanded; the articular surface is broadly rounded. There is a prominence on the internal surface about one-third of the total length from the distal end. Along the external side of the bone there is a blunt keel for about the distal half of the shaft.

Measurements

		mm.
Left radius:	length................................	79
	maximum width at proximal end..........	17.2
	maximum width at distal end............	11.3

Ulnae (Plate XII, figs. 5, 7). The ulna is expanded at both ends. The proximal extremity is thick, trianguloid in cross-section, and has a short and blunt olecranon. The shaft is flattened from midlength distally. The distal end is flat, but with a low keel on the ventral side. The terminal or articular surface is almost straight.

Measurements

		mm.
Left ulna:	length................................	83.5
	maximum width at proximal end............	22.3
	maximum width at distal end..............	23.1

Carpals (Plate XII, fig. 7). Seven elements of the carpus are preserved. There is no intermedium, no pisiform, no fifth carpale. These may have been cartilaginous, but it seems more likely that they were lost during burial. The other elements do not articulate closely. The *radiale* is a flat bone, roughly triangular in outline. The dorsal and ventral surfaces are

at an angle to each other, so that they meet as an edge along the inner margin. The proximal end tapers to a blunt point. The distal end is truncated obliquely and is fused to the centrale. The *centrale* is wider than long, and its outline tapers to a blunt point on the external side. The distal articular surface is rounded. The *ulnare* is roughly rectangular in outline, longer than wide, and slightly concave on the dorsal and ventral surfaces. There is a narrow flattened surface along the external margin, but the internal margin is angulate. The proximal articular end is flat, the distal end obliquely truncated at its two corners, and the remaining surface fused to the fourth carpale. The *fourth carpale* is rectangular in outline, wider than long. It is slightly concave on the dorsal surface and flat on the ventral. All margins have flattened surfaces. The distal margin is oblique, so that the bone is longer on its outer side than on its inner. The *third carpale* is rounded-cuboid in shape, the flattest surface being the distal one. The *second carpale* is small, roughly ellipsoidal in shape, wider than long. The *first carpale* is only slightly larger than the second, is rounded, and tapers to a blunt point on the internal side.

Measurements

		mm.
Left radiale:	length	16.5
	width	12.6
Left ulnare:	length	15.0
	width	12.8
Left centrale:	length	9.0
	width	12.6
Left first carpale:	length	7.5
	width	7.8
Left second carpale:	length	5.7
	width	7.8
Left third carpale:	length	7.8
	width	8.6
Left fourth carpale:	length	8.6
	width	11.0

Metacarpals (Plate XII, fig. 7). These are elongate bones, especially the second, third, and fourth. The proximal ends are expanded and somewhat rounded, the distal ends less expanded, and flattened. The first and fifth metacarpals are subequal in length and shorter than the others. The first metacarpal on the left manus has a narrow ovoid foramen in the ventral surface, a little proximal from midlength. This portion is not preserved in the right manus.

Measurements

		mm.
Left first metacarpal:	length	20.1
	width	9.6
Left second metacarpal:	length	33
	width	11.8
Left third metacarpal:	length (estimated)	35
	width	13.1
Left fourth metacarpal:	length	31.7
	width	11.7
Left fifth metacarpal:	length	20.3
	width	10.7

Phalanges (Plate XII, fig. 7). The following phalanges are preserved on one or both feet: first digit, none; second digit, none; third digit, two;

fourth digit, three; fifth digit, three. The formula is believed to be 2, 3, 4, 5, 4, as the three phalanges of the fifth digit do not include the ungual. All of the phalanges present are elongate and slender, slightly constricted toward midlength. They are progressively shorter from proximal to distal.

Measurements

		mm.
First phalanx, left third digit:	length	18.0
	width	9.3
Second phalanx, left third digit:	length	14.0
	width	7.9
First phalanx, left fourth digit:	length	16.3
	width	8.7
Second phalanx, left fourth digit:	length	13.0
	width	7.1
Third phalanx, left fourth digit:	length	11.7
	width	6.9
First phalanx, left fifth digit:	length	12.0
	width	6.6
Second phalanx, left fifth digit:	length	9.7
	width	5.1
Third phalanx, left fifth digit:	length	8.4
	width	3.6

POSTURE

Plate I, fig. 1, shows a photograph of specimen No. 8919 as mounted for exhibition. All portions posterior to the eleventh dorsal vertebra are plaster restorations. The posture selected is based in part on experiments by Dr. Langston, and the result is a very animated pose. However, a number of problems were encountered, which were not satisfactorily solved. The position of the humerus, although the best that could be selected, seems mechanically poor, especially from the standpoint of manipulation. The hind limbs appear better adapted to support than the front limbs, a condition found in archosaurs, but not a condition characteristic of the more primitive diapsids. When the pelvic symphysis is closed, the intra-pelvic space seems much too small. In life there may have been a symphysial gap, occupied by cartilage. The parasternal ribs project laterally beyond the extremities of the dorsal ribs and, when aligned with the posterior ventral portion of the pectoral girdle, leave a lateral gap between them and the dorsal ribs. It might be assumed that the parasternal ribs originally had a strong curvature upward on either side, and that they have been flattened by pressure during fossilization. However, the dorsal ribs show little evidence of flattening. The specimens described by Brown and Parks also show the wide, flat array of parasternal ribs.

PROBABLE HABITS

The general resemblance of the skeleton of *Champsosaurus* to that of the gavial crocodile suggests similar life habits, that is to say, aquatic and fish-eating. This is supported by many characteristic features of *Champsosaurus*. The slender, relatively weak jaws were operated by powerful temporal muscles, with greatly expanded origin areas on the skull. As the jaws could not have served to chew tough food, the function of the powerful

musculature must have been to achieve a quick snap. Long, slender jaws with many sharp teeth are characteristic of fish-eating vertebrates, such as *Lepidosteus*, *Esox*, and *Gavialis*, and of presumed fish-eaters like the ichthyosaurs, mesosaurs, and phytosaurs.

The loose articulation of the vertebral column and limbs suggests that *Champsosaurus* spent almost all of its time in the water, perhaps coming ashore only to lay its eggs. The amphiplatyan vertebral centra, the moderately developed zygopophyses, and the lack of fusion between centra and neural arches all indicate a weak vertebral column. The front limbs seem more adapted to horizontal movement than to vertical support. The pelvis is loosely articulated with the sacral vertebrae, and the pubes and ischia probably had a cartilaginous symphysis. The distal thickening of the dorsal ribs suggests the condition in sirenians, and the extensive and flat cuirasse of parasternal ribs is like that of plesiosaurs.

The accompanying restoration (Plate I, fig. 2) is an attempt to portray the living *Champsosaurus* in a swimming pose. The main thrust is given by hind limbs and tail. The suggestion of a median frill is in keeping with conditions in some crocodiles and lizards, and in *Sphenodon*.

The association of *Champsosaurus* remains, within the fossil deposits, should be considered in any postulation of life habits. The vertebrae of this reptile are characteristic elements of the familiar bone-bed assembly, which also includes the scales of *Lepidosteus*, the teeth of the fresh-water ray *Myledaphus*, and less numerous fragments representing sturgeons, bow-fins, and salamanders. Teeth and small bones of crocodiles and dinosaurs are also present, suggesting that these deposits are the end products of some transportation and sorting. Thus the association of *Champsosaurus* remains does not prove the aquatic habitat, but it is strongly suggestive of such a mode of life.

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Illustrations

PLATE I

Figure 1. *Champsosaurus natator*, N.M.C. No. 8919, mounted skeleton and restoration. Skeleton is restored posterior to twentieth vertebra. About X $\frac{1}{6}$.

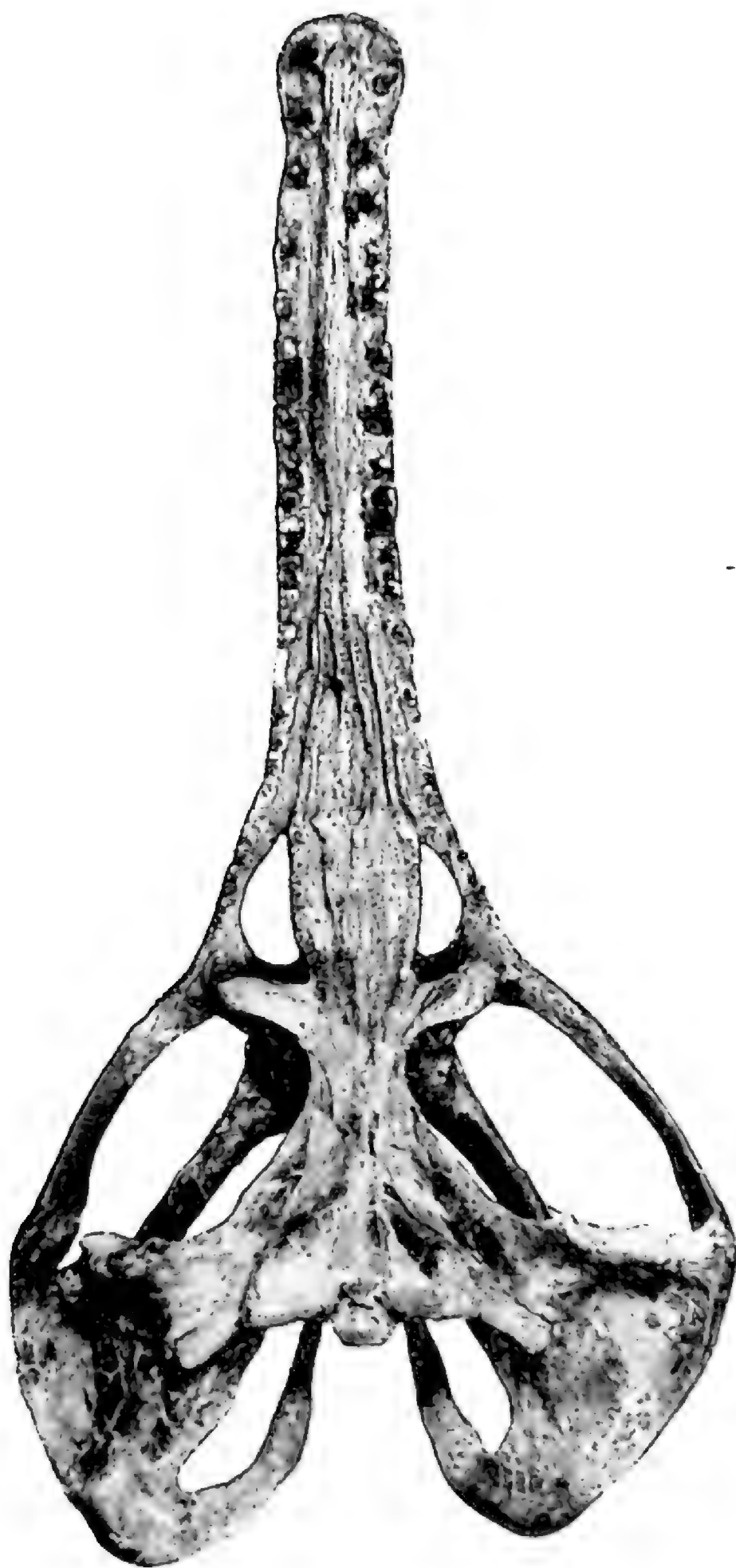Figure 2. Life restoration of *Champsosaurus* in swimming posture.

PLATE I

1

2
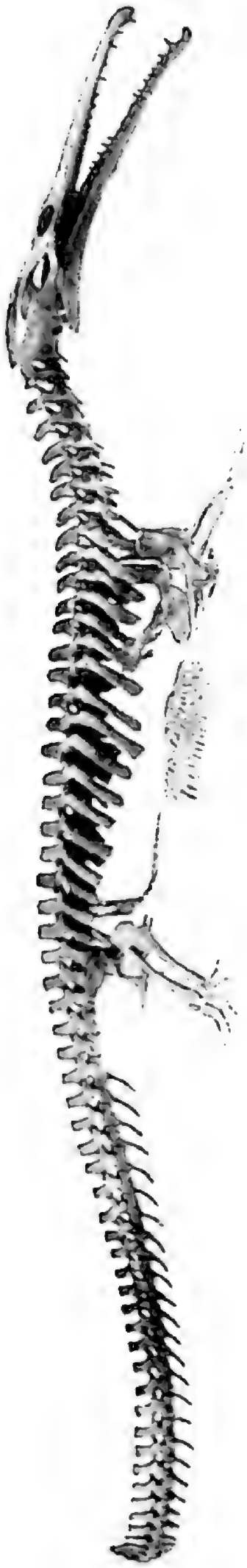
PLATE II

Champsosaurus natator, N.M.C. No. 8919, dorsal view of skull. X ⅓.

Plate III

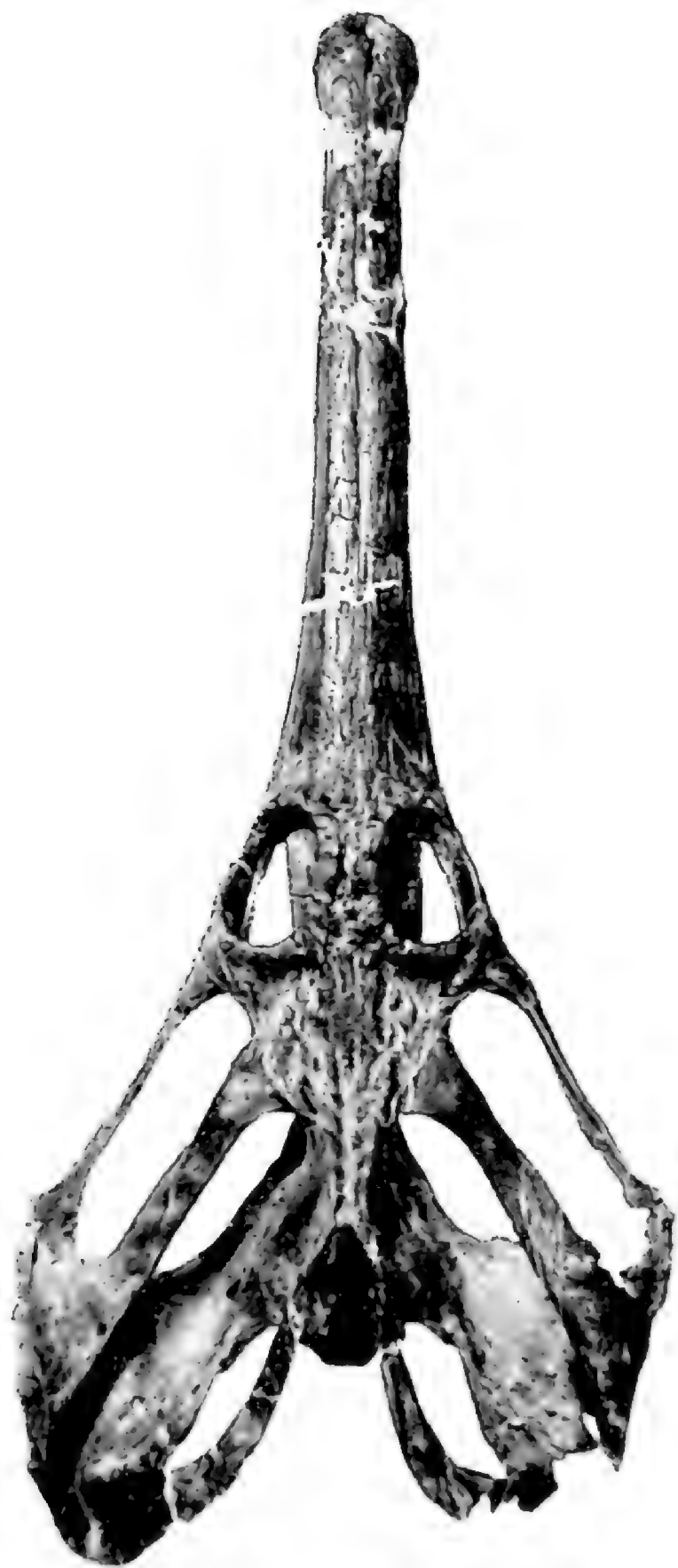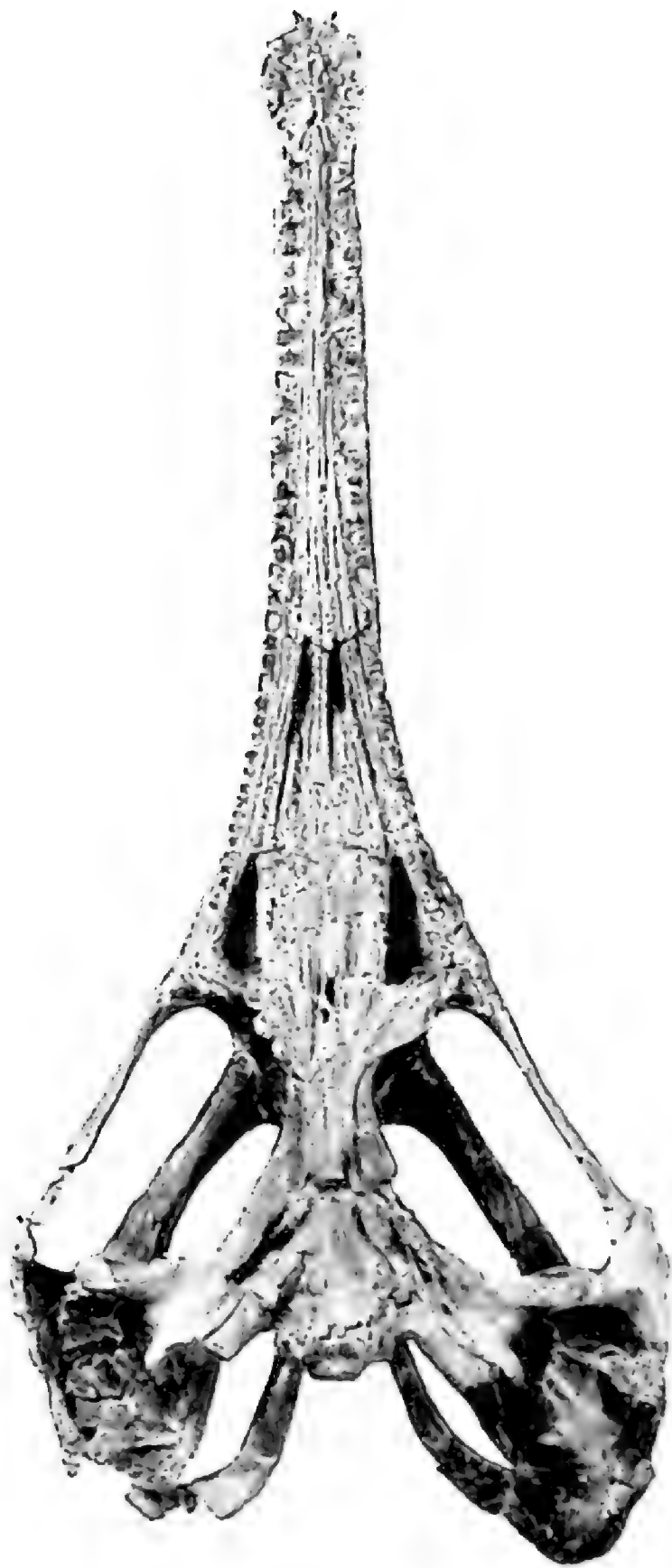*Champsosaurus natator*, N.M.C. No. 8919, ventral view of skull.   X ⅓.

PLATE III

PLATE IV

PLATE IV

Champsosaurus natator, N.M.C. No. 8920, dorsal view of skull. X ½.

PLATE V

Champsosaurus natator, N.M.C. No. 8920, ventral view of skull.   X ½.
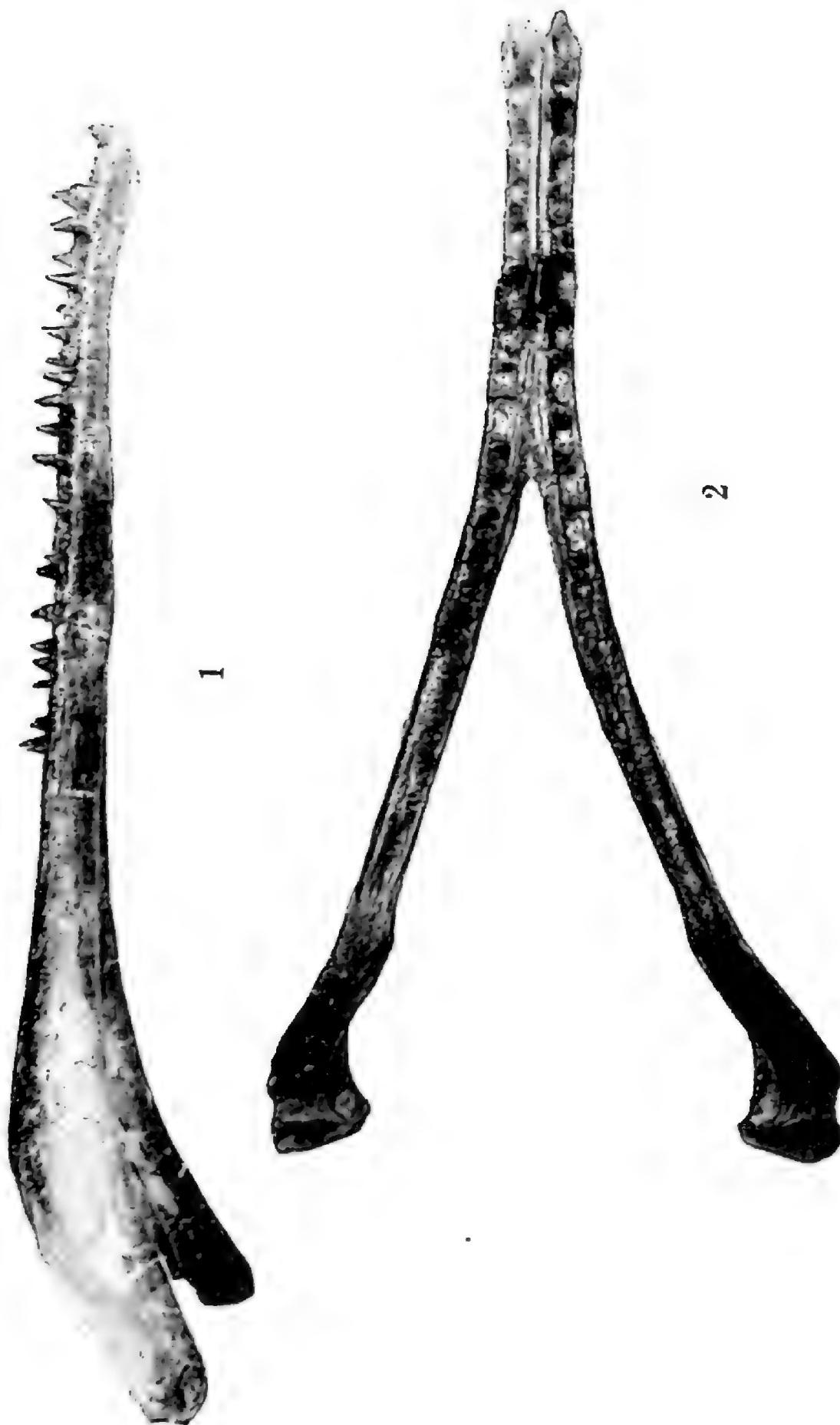
PLATE V

Plate VI

PLATE VI

Champsosaurus natator, N.M.C. No. 8919, mandible.   C.   X ⅓.

    Figure 1.   Right lateral view.

    Figure 2.   Dorsal view.

PLATE VII

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure 1. Hypocentrum of second vertebra, left lateral view

Figure 2. Same, posterior view.

Figure 3. Neural arch of second vertebra, anterior view (with restored centrum).

Figure 4. Same, left lateral view.

Figure 5. Same, posterior view.

Figure 6. Third vertebra, anterior view.

Figure 7. Same, left lateral view.

Figure 8. Same, posterior view.

Figure 9. Fourth vertebra, anterior view.

Figure 10. Same, left lateral view.

Figure 11. Same, posterior view.

Figure 12. Fifth vertebra, anterior view.

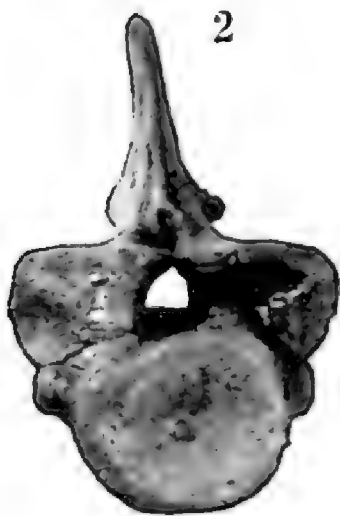Figure 13. Same, left lateral view.

Figure 14. Same, posterior view.

Figure 15. Sixth vertebra, anterior view.

Figure 16. Seventh vertebra, anterior view.

Figure 17. Eighth vertebra, anterior view.

Figure 18. Ninth vertebra, anterior view.

PLATE VII

3   6   9   12

1   4   7   10   13

2   5   8   11   14

15   16   17   18

42
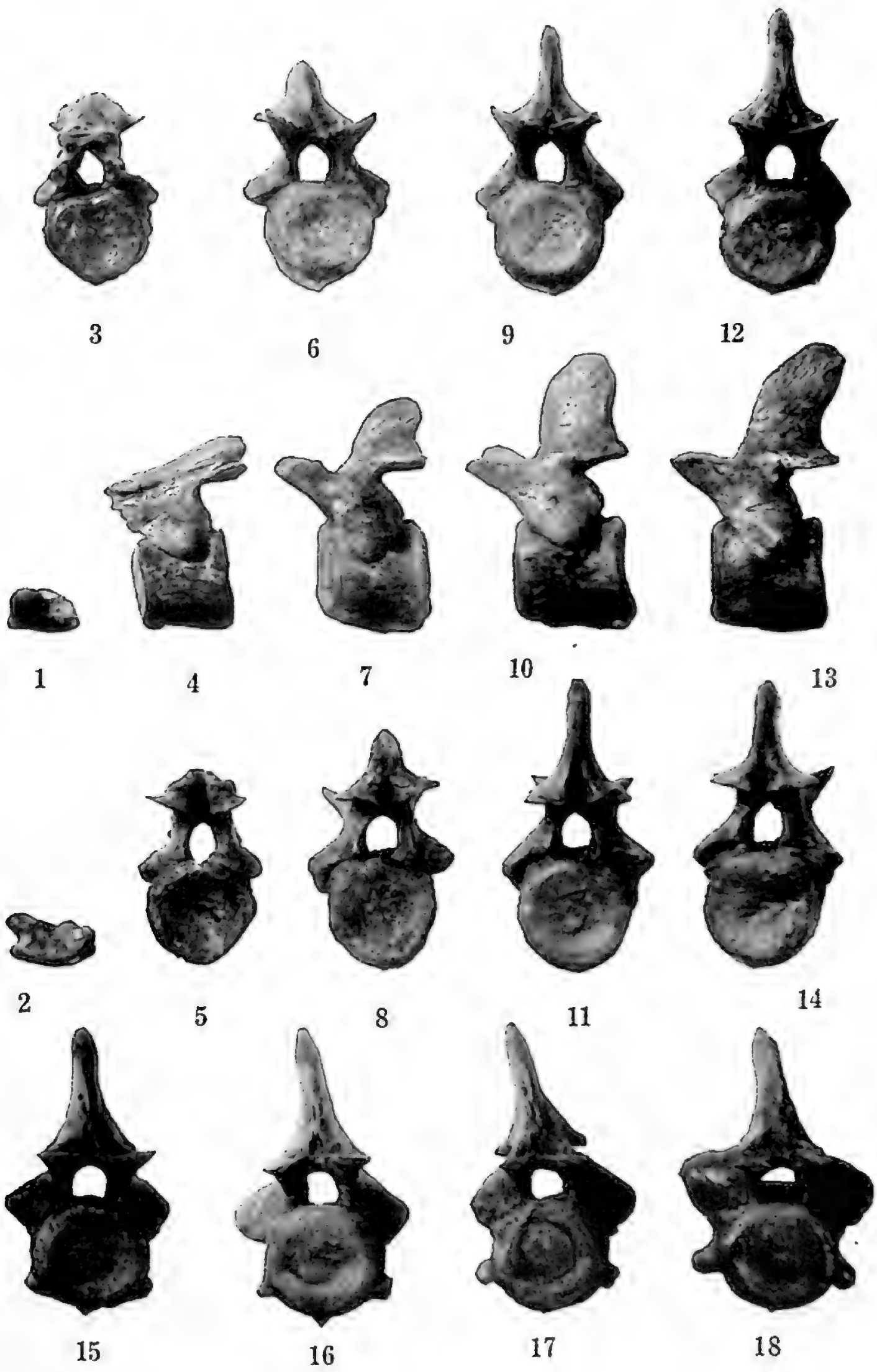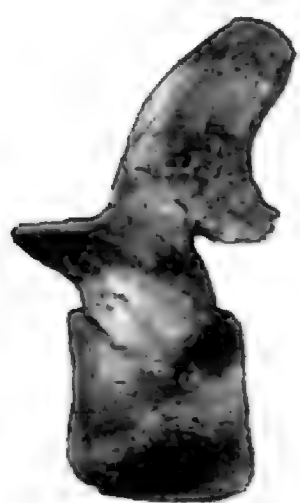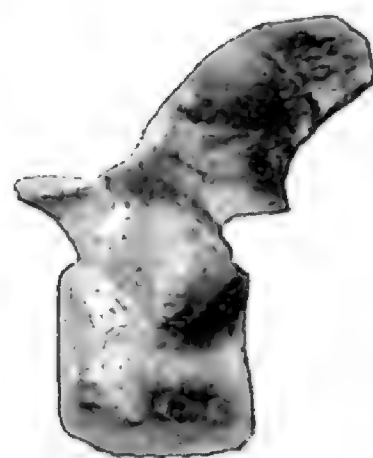
PLATE VIII

1   3   5   7
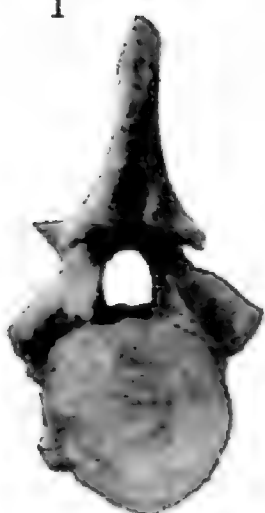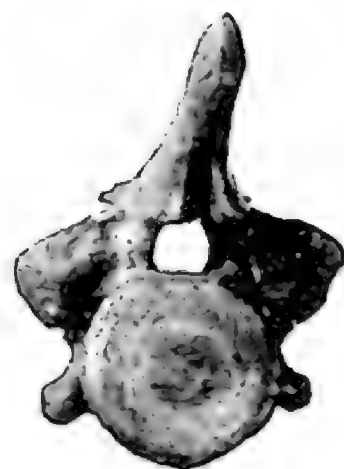
2   4   6   8
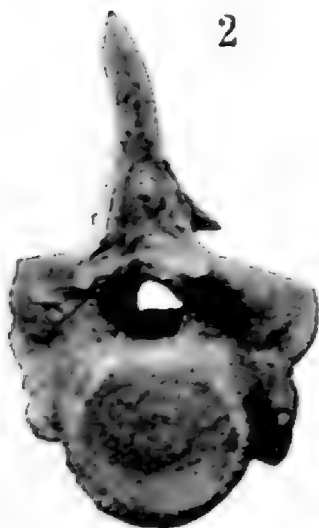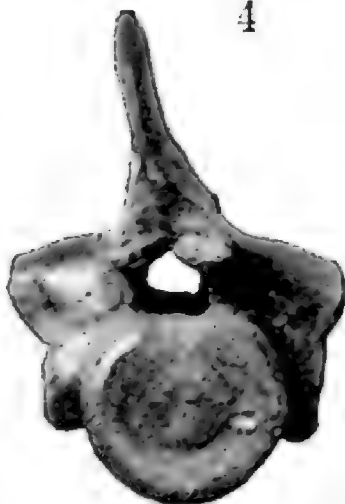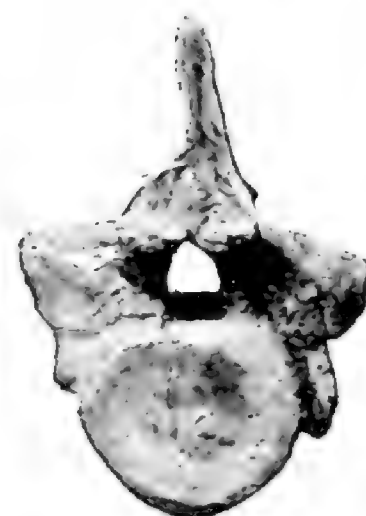
9   11   13   15

10   12   14   16

PLATE VIII

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure   1.   Sixth vertebra, left lateral view.

Figure   2.   Same, posterior view.

Figure   3.   Seventh vertebra, left lateral view.

Figure   4.   Same, posterior view.

Figure   5.   Eighth vertebra, left lateral view.

Figure   6.   Same, posterior view.

Figure   7.   Ninth vertebra, left lateral view.

Figure   8.   Same, posterior view.

Figure   9.   Tenth vertebra, anterior view.

Figure 10.   Same, left lateral view.

Figure 11.   Eleventh vertebra, anterior view.

Figure 12.   Same, left lateral view.

Figure 13.   Twelfth vertebra, anterior view.

Figure 14.   Same, left lateral view.

Figure 15.   Thirteenth vertebra, anterior view.

Figure 16.   Same, left lateral view.

PLATE IX

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure 1.   Tenth vertebra, posterior view.

Figure 2.   Eleventh vertebra, posterior view.

Figure 3.   Twelfth vertebra, posterior view.

Figure 4.   Thirteenth vertebra, posterior view.

Figure 5.   Fourteenth vertebra, anterior view.

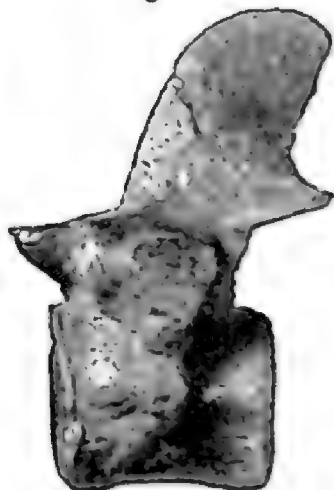Figure 6.   Same, left lateral view.

Figure 7.   Same, posterior view.

Figure 8.   Fifteenth vertebra, anterior view.

Figure 9.   Same, left lateral view.

Figure 10.   Same, posterior view.

Figure 11.   Sixteenth vertebra, anterior view.

Figure 12.   Same, left lateral view.

Figure 13.   Same, posterior view.

Figure 14.   Seventeenth vertebra, anterior view.

Figure 15.   Same, left lateral view.

Figure 16.   Same, posterior view.

PLATE IX
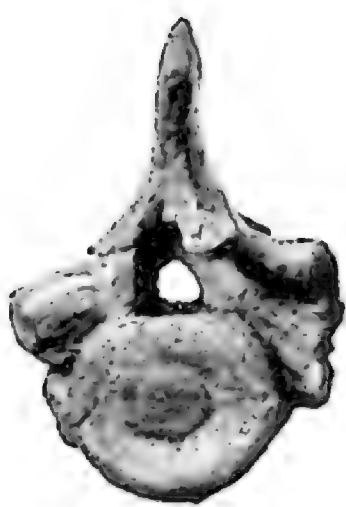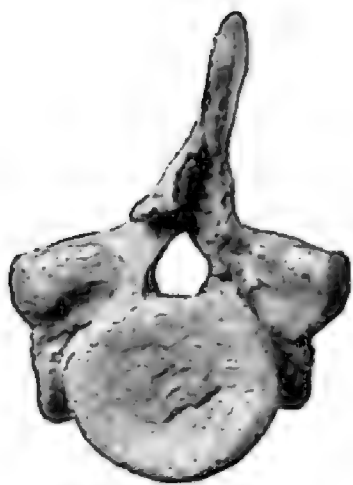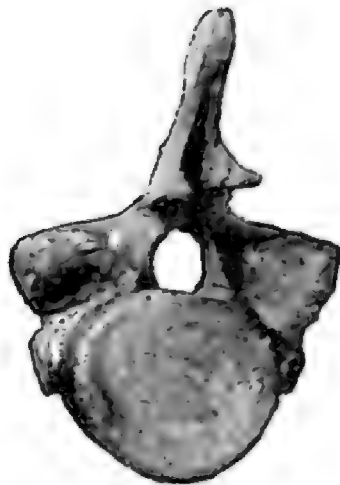
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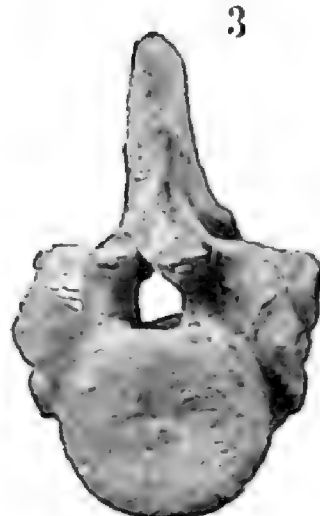
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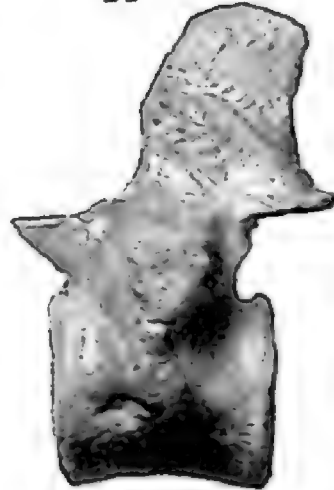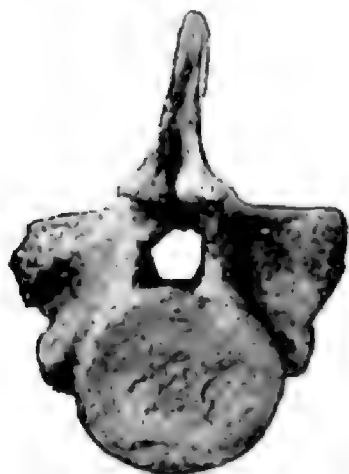
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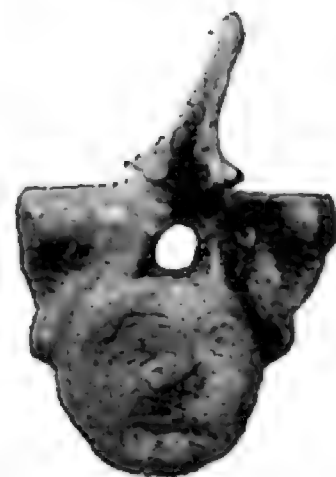
PLATE X
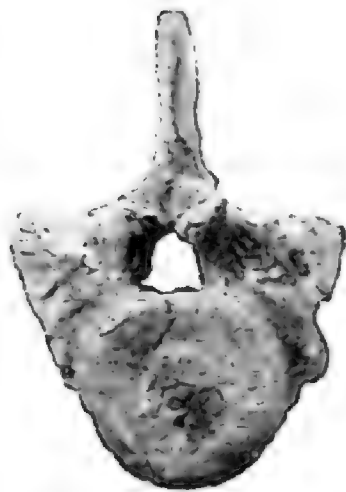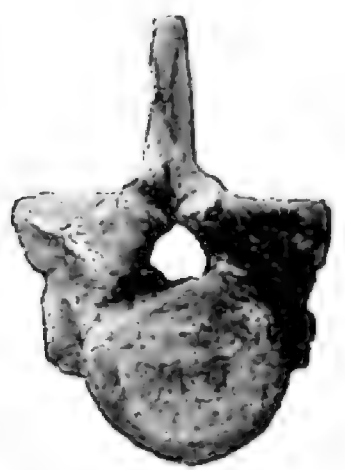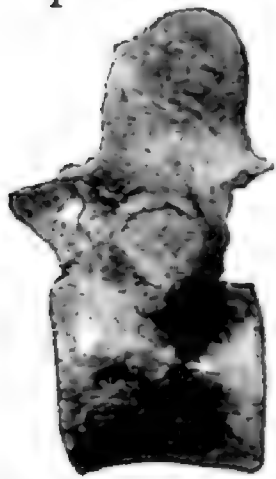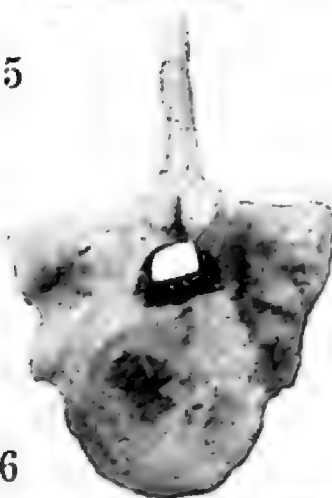
PLATE X

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure 1.   Eighteenth vertebra, anterior view.

Figure 2.   Same, left lateral view.

Figure 3.   Same, posterior view.

Figure 4.   Nineteenth vertebra, anterior view.

Figure 5.   Same, left lateral view.

Figure 6.   Same, posterior view.

Figure 7.   Twentieth vertebra, anterior view.

Figure 8.   Same, left lateral view.

Figure 9.   Same, posterior view.

Figure 10.   Sixth left rib, lateral view.

Figure 11.   Seventh left rib, lateral view.

Figure 12.   Eighth left rib, lateral view.

Figure 13.   Ninth left rib, lateral view.

Figure 14.   Tenth left rib, lateral view.

Figure 15.   Eleventh left rib, lateral view.

Figure 16.   Twelfth left rib, lateral view.

PLATE XI

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure 1.   Thirteenth left rib, lateral view.

Figure 2.   Fourteenth left rib, lateral view.

Figure 3.   Fifteenth left rib, lateral view.

Figure 4.   Sixteenth left rib, lateral view.

Figure 5.   Seventeenth left rib, lateral view.

Figure 6.   Eighteenth left rib, lateral view.

Figure 7.   Clavicles and interclavicle, dorsal view.

Figure 8.   Same, ventral view.

1   2   7   3

4   8   5   6
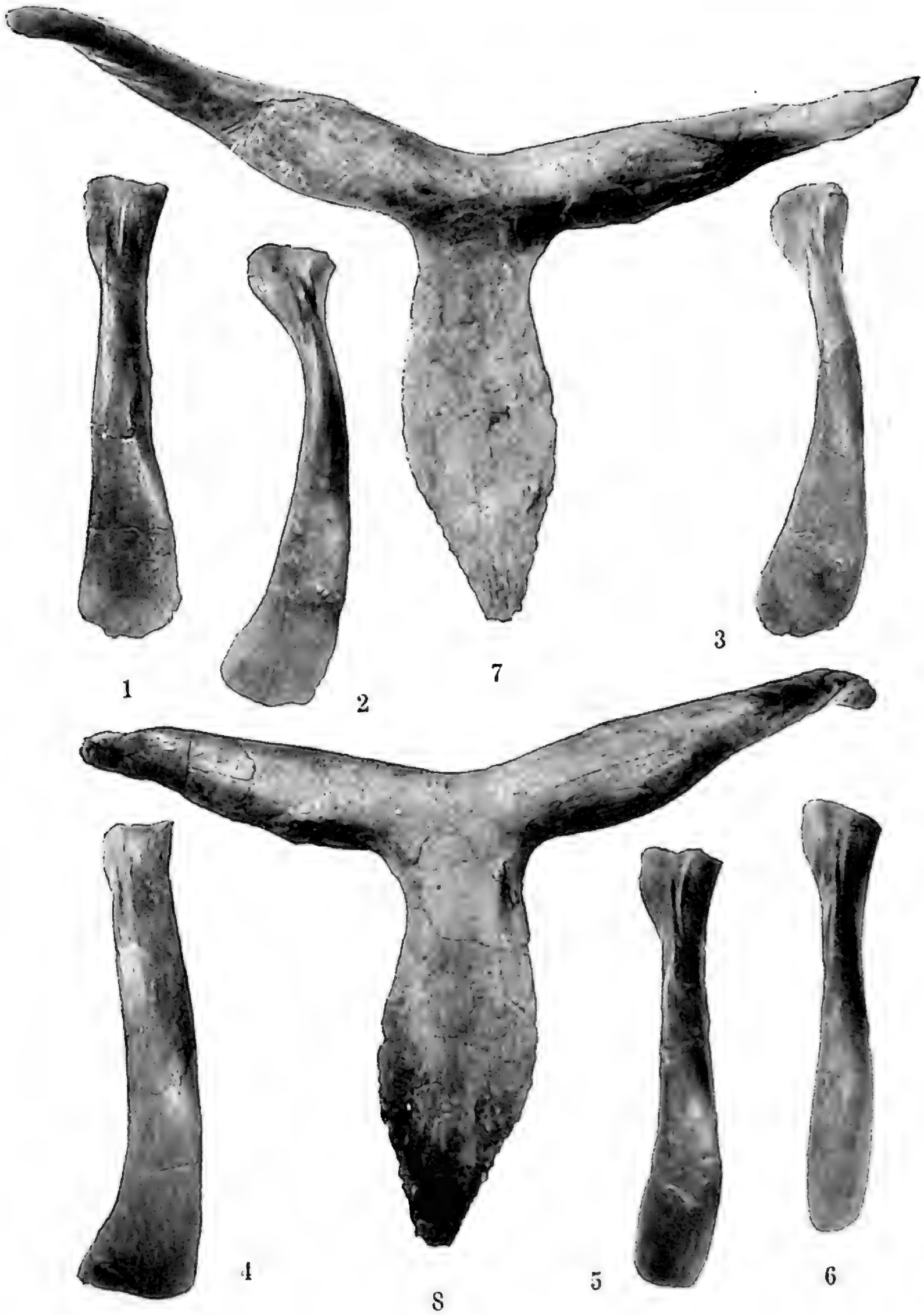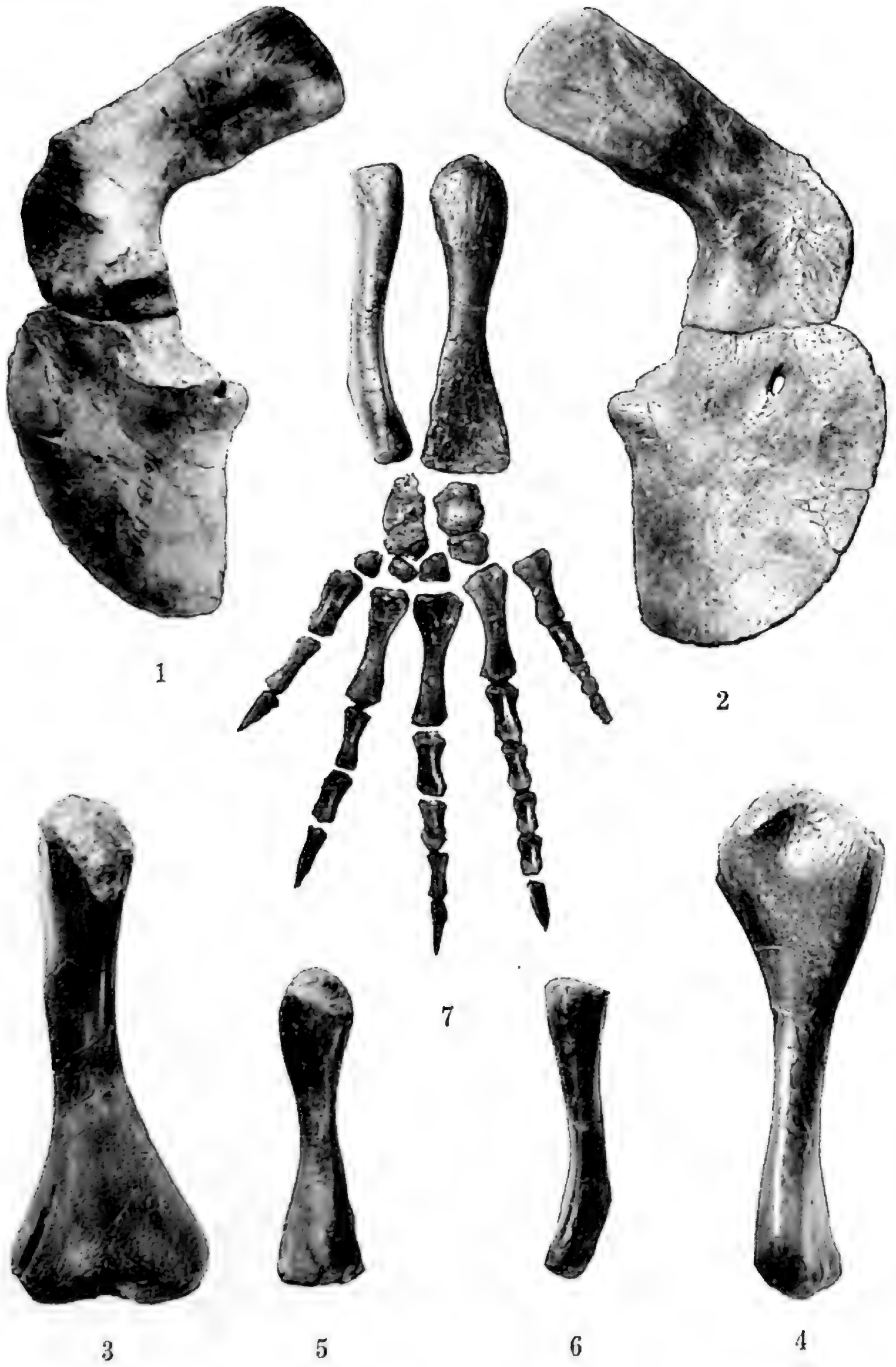
Plate XII

Plate XII

PLATE XII

Champsosaurus natator, N.M.C. No. 8919.   X ½.

Figure 1.   Left scapula and coracoid, ventral view.

Figure 2.   Same, dorsal view.

Figure 3.   Left humerus, preaxial view.

Figure 4.   Same, postaxial view.

Figure 5.   Left ulna, preaxial view.

Figure 6.   Left radius, preaxial view.

Figure 7.   Left front foot with radius and ulna, dorsal view.
(most of the phalanges are restored; see text).